THE DEVELOPMENT OF SOCIAL BEHAVIOUR IN PIGLETS

by

Ruth Catriona Margaret Hutton BSc(Hons)

A thesis submitted for the degree of
Doctor of Philosophy

University of Edinburgh

1983

This thesis has been composed by me and is a record of my own work.

ABSTRACT

In the first part of this thesis, the behavioural development of domestic piglets kept in a socially and ecologically rich outdoor environment, the Pig Park, is traced. In the second part, the effects on behaviour of artificially rearing piglets in individual incubators for their first seventeen days are examined. By contrast with the Pig Park, the incubators provided a very barren and restricted environment. Focal animal and scan sampling techniques were used to collect data, which was then subjected to frequency, sequence and cluster analyses.

In the Pig Park, piglets remained in and around their farrowing nest during their first week, after which they started to rest in other nests and to interact with other pigs. After the formation of teat preferences, they were mainly responsible for locating and defending their teat from other piglets. Two piglets switched mothers when they were two and six weeks old respectively, while others sometimes suckled opportunistically from vacant teats other than their own. Piglets were aware of the activities of those around them and social facilitation occurred, especially between littermates. Weak dominance relationships were demonstrated between pairs of piglets, but the outcome of an interaction also seemed to be affected by the context and the motivation of the participants. Social interactions and spatial associations were more likely to occur with the dam or a piglet than with a juvenile or other adult. Within litters, strong and lasting preferences for particular individuals were not found. Locomotory play was the most common form of play, especially between three and six weeks of

age. The observations are discussed with reference to the selection pressures acting on wild piglets and the degree to which behaviour has been modified through domestication.

In the incubators, high levels of high-pitched vocalization were attributed to frustration induced by an unpredictable supply of milk. Stereotyped rooting and biting, and massaging of the nipple drinker were also observed. When transferred to flat-deck cages and placed in pairs, the piglets showed abnormally high levels of many social behaviour patterns, including massaging, sucking, levering and circling. With time, their behaviour became similar to that of control piglets reared by sows, with the exception that only incubator-reared piglets massaged their nipple drinker. The results are related to the welfare of piglets and the effects of environment on motivation and behaviour.

CONTENTS

CONTENTS (continued)

CONTENTS (continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF TABLES

LIST OF PLATES

GENERAL INTRODUCTION

Most studies on the behaviour of domestic piglets have provided descriptions of behaviour under the limited range of environments currently popular with pig producers, such as farrowing crates and flat-deck cages. These environments are usually physically restricted and barren (unchanging, lacking in a variety of stimuli), and the piglet is limited to social contact with its mother and littermates prior to artificial weaning, followed by like-aged piglets after weaning. In order to obtain a more thorough understanding of the behaviour of piglets, it is necessary to investigate the range of behaviour occurring in natural settings. By this means, it may be possible to obtain an indication of the extent to which their behaviour has become modified through domestication from that of their main ancestor, the European wild boar (*Sus scrofa*). It is possible that many behaviour patterns may have been altered genetically, through changes in the thresholds at which they are performed and changes in responses to certain stimuli (Wood-Gush, 1983), during artificial selection for piglets adapted to life in confined and barren environments.

As Signoret *et al.* (1975) point out, there is a great need for studies on domestic pigs kept under 'free-range' conditions. Only by giving piglets the opportunity to exhibit their full behavioural repertoire is it possible to determine the extent to which the rearing of piglets in intensive housing conditions affects their behaviour, and to interpret their behaviour in the absence of natural stimuli and substrates. Therefore, in the first part of this study, piglets of a common agricultural breed, the Large White, were observed under free-range conditions in the Pig Park, which

provides a spacious, physically and socially complex environment (Plate 1). The aim was to describe their behavioural development and social relationships, thereby providing a basis for comparison with more socially and physically restricted environments.

By contrast to the rearing of piglets in a semi-natural environment, there is a move among pig producers towards the rearing of piglets under highly artificial conditions (Lecce, 1971; Fowler and Varley, 1980). At the Rowett Institute in Bucksburn, Aberdeen, an early-weaning unit has been set up in which Large White piglets are weaned from their mothers at one day of age and reared artificially in individual incubators for two to three weeks before being transferred to flat-deck cages for rearing in pairs. Little is known about the effects on behavioural development of rearing under such conditions, but it was expected that the behaviour of these piglets would be very different from that of the Pig Park piglets. In the second part of this study, behavioural data obtained at the Rowett Institute from artificially reared piglets is described and compared with that from the Pig Park in order to indicate the range of behaviour which can occur in domestic piglets and the ways in which behavioural development may be modified by rearing in a very barren and confined environment. Particular attention is paid to the effects of early social isolation on later social behaviour.

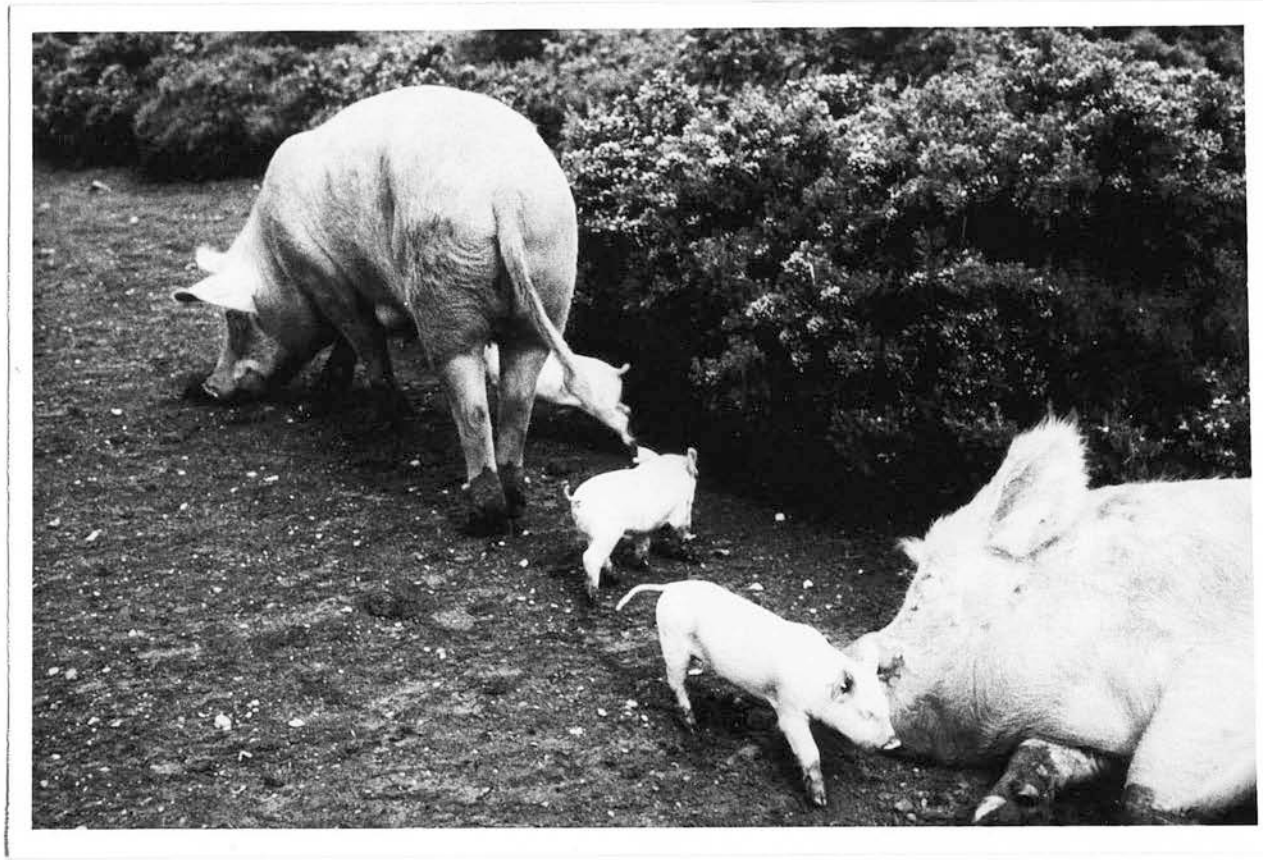

Plate 1 A sow (WB) sniffs the ground as she walks slowly up a wide path between gorse bushes in the Pig Park. Her two week old piglets scamper between her and an adult boar (7) who lies resting on his side

PART 1 - THE PIG PARK

INTRODUCTION

With the aim of describing the behavioural development and social relationships of piglets living in the Pig Park, a series of questions were asked with reference to the relevant literature. These are now described.

Suckling behaviour

The suckling behaviour of intensively-reared piglets has received much attention in connection with its relation to birth weight, growth rate, the formation and maintenance of a teat order, the effect of fostering piglets and the frequency of sucklings with and without milk let-down. Gill and Thomson (1956) found that individual sows tended to suckle in a characteristic position, either standing or lying on a particular side. In sows which lay on one side, piglets suckling from the upper row of teats obtained more milk than those suckling from the lower row. Sows which stood to suckle produced less milk than those which lay, possibly because their piglets could not massage their teats as forcibly. A positive correlation was found between time spent massaging and milk yield. In addition, the four piglets suckling nearest to the anterior end of the udder received 15.3% more milk than the four nearest to the posterior end. McBride *et al.* (1965), Fraser and Morley-Jones (1975), Harstock *et al.* (1977), Fraser *et al.* (1979) and Campbell and Dunkin (1982) also found small positive correlations between suckling from anterior teats and relatively high weights at three weeks of age, although relative birth weight within the litter had a much larger effect on three week weight. It was therefore of

interest to determine how the position of the sow, and the location of piglets along the udder affected the growth rates of piglets in the Pig Park.

From the day of birth, piglets show individual preferences for particular teats along the sow's udder and may fight with others for mutually favoured teats. Within one (McBride, 1963) to two weeks (Hemsworth *et al.*, 1976), a stable teat order has developed, whereby each piglet suckles primarily from its 'own' teat and defends it from others. Fostering of piglets is best accomplished within the first two days of life, before the development of a strong attachment to a particular teat (Hosman, cited in Signoret *et al.*, 1975). After this, a fostered piglet will fight with the resident owner for its favoured teat in the corresponding position on the foster mother's udder (Horrell and Bennett, 1981). In the Pig Park, the development and maintenance of the teat order was examined, with particular reference to the possibility of cross-suckling occurring between piglets from different litters.

Physical stimulation of the anterior teats is important in eliciting milk let-down (Fraser, 1973, 1975a), and a greater preference for anterior teats shown by piglets in some studies may be due to greater ease in obtaining milk from these teats and/or their possibly higher milk yield. It has been suggested that piglets fight to gain possession of more anterior teats and that the teat order is a dominance hierarchy (Wilson, 1975; Pond and Houpt, 1978). However, due to the great variation found between preference for, and weight gain on, different teats, and due to the fact that piglets tend to develop an early preference for a certain location on the udder and fight mainly for teats within that area

(Hemsworth *et al.*, 1976; Jeppesen, 1980), it cannot be assumed that piglets suckling from the anterior teats are the most successful competitors for the best teats. On the other hand, Scheel *et al.* (1977) did find that piglets successful in fights for teats at any position along the udder were also likely to be successful in fights away from the udder at an older age. Therefore, in this study observations of the outcomes of fights at and away from the udder in the Pig Park were compared.

In intensive housing systems, sucklings occur at intervals of 48 to 54 minutes during the first week, declining to 57 to 68 minutes during the eighth week (Barber *et al.*, 1955). Not all sucklings result in the let-down of milk and Fraser (1977) found that if a suckling was initiated within 40 minutes of the last successful suckling (i.e., with milk let-down), it was more likely to be unsuccessful than if initiated after a longer interval. The mean interval between two consecutive successful sucklings was 53.2 minutes, but this increased to 75.7 minutes if two successful sucklings were interspersed by one or more unsuccessful sucklings. These results were obtained in a noisy modern farrowing house where the sows were confined in farrowing crates. Whatson (1979) housed sows in an unrestricted condition in a large, quiet room, but this did not significantly reduce the percentage of unsuccessful sucklings compared with that of sows kept in farrowing crates. The mean for both conditions was 27%. As it would conceivably be uneconomical for wild sows to waste time suckling piglets at times when milk let-down is unlikely to occur, it was of interest to look at the frequency of successful and unsuccessful sucklings in the Pig Park, and to determine the factors involved in the initiation and termination

of suckling bouts.

Finally, as intensively-reared piglets are weaned artificially by removal from the sow at ages varying between birth and six weeks, the factors associated with natural weaning cannot be examined. Observations in the Pig Park were aimed at determining when weaning occurred naturally, whether it varied between litters and between individuals within litters and whether aggression from the sow was the main factor initiating the weaning process.

Resting behaviour

The thermoregulatory response of piglets is not fully developed until their twentieth day (Holub *et al.*, 1957). They compensate for their large body surface to volume ratio and low levels of subcutaneous fat and body hair by huddling together in contact with other piglets and their mother. By lying on their bellies with their legs tucked under them, they can also conserve body heat when compared with lying stretched out on their sides (Mount, 1968).

In wild pigs (Hanson and Karstad, 1959; Kurz and Marchinton, 1972; Frädich, 1974; Mauget, 1982), sows build nests shortly before farrowing and the piglets remain in and around the nest for up to three weeks after birth. At this time, several sows with litters may associate and rest together in a common nest. Adult boars are usually solitary, joining groups of sows during the autumn and winter for mating (and at other times if two litters are produced per year). The births of sows belonging to the same group are synchronized within 10 to 15 days, and juvenile offspring from their previous litters are said to leave at this time, although it is not clear how far they go or whether the females rejoin their

mothers when they become pregnant.

Familiarity appears to be an important factor determining who rests with whom in domestic pigs. In the Pig Park, Stolba (1982) found that two groups of pigs previously kept in separate enclosures continued to rest in separate nests for over 190 days when both groups were kept in the same enclosure. Also, Signoret *et al.* (1975) report that familiar pigs and littermates tend to rest together after the mixing of large numbers of animals in stockyards.

In this study, the amount of time spent resting in different positions both in and out of contact with others was investigated, and the factors affecting the choice of different resting sites and resting companions were examined.

Social facilitation

A previous study (Hutton, 1979) showed that adults and juveniles in the Pig Park sometimes synchronized their performance of various behaviour patterns (e.g., grunting, rubbing and scratching). The individuals most likely to synchronize their activities tended to be those with the strongest social relationships as determined by other measures, which suggested that some influence was passing between individuals during the performance of apparently non-social behaviour patterns.

The term 'social facilitation' has been used by many authors to refer to a variety of phenomena, including synchronization of group activities (Kummer, 1971; Tyler, 1972), increments of food intake (Tolman, 1964) and running speed (Scott and Marston, 1950) in the presence of conspecifics, and the contagious performance of instinctive behaviour patterns (Thorpe, 1963). However, the term is used

here in a purely descriptive sense to refer to 'the performance of a pattern of behaviour already in an individual's repertoire, as a consequence of the performance of the same behaviour by other individuals' (Hinde, 1970, p. 582).

It was decided to use relative levels of social facilitation between piglets to look for early social preferences and to determine whether these changed during development. The relative amount of social facilitation between individuals was measured using cluster analysis techniques (Jardine and Sibson, 1968; Morgan *et al.*, 1976) on inter-individual bouts of particular behaviour patterns.

Dominance

In intensive housing systems, dominance hierarchies are formed and maintained after the mixing of unfamiliar weaned and adult pigs (McBride *et al.*, 1964, 1965; Meese and Ewbank, 1973a). Smell and vision are important in the recognition of unfamiliar individuals (Ewbank *et al.*, 1974). Once formed dominance relationships remain fairly stable, although spontaneous changes do occur (Meese and Ewbank, 1972). High social status is positively correlated with relatively high weight (McBride *et al.*, 1964, 1965; Scheel *et al.*, 1977) as well as male gender (Beilharz and Cox, 1967; Scheel *et al.*, 1977). Also, piglets with upright ears (Large White type) tend to dominate those with floppy ears (Landrace type) according to Fraser (1974).

However, dominance relationships have been measured in a variety of ways. Fraser (1974) considered an individual to be dominant over another if it directed vigorous bites towards the other and the other did not bite back. Dominance is often equated

with priority of access to resources, but in the case of fights between strangers and fights in the absence of any obvious immediate reward, priority of access may or may not be a delayed advantage of winning fights. Also, different animals may have priority of access to different resources (Bernstein, 1970; Rowell, 1974). Beilharz and Cox (1967) considered a pig to be dominant over another if it exhibited priority of access to food, but results may have differed if the animals had been competing for teats or for females in heat. In addition, Meese and Ewbank (1973b) found no correlation between social rank (as measured by the direction of aggression while feeding) and leadership or exploratory activity.

Measures of dominance which involve the relative level of aggressiveness between individuals (e.g., Rasmussen *et al.*, 1962) or the outcome of aggressive encounters (e.g., Scheel *et al.*, 1977) may only be of value in predicting priority of access to a resource if aggressive acts are observed between all dyads in the group and if the direction of the outcomes remain constant over a number of interactions. However, Ewbank and Bryant (1972) obtained higher levels of aggression and more retaliations by low ranking animals as pigs were kept under increasingly crowded conditions. Also, Jensen (1982) found that in sows kept in relatively unconfined groups indoors as well as outdoors in the Pig Park (Jensen and Wood-Gush, in press), overt aggression was low and dominance hierarchies were maintained mainly as a result of avoidance of low ranking individuals. In crowded conditions, space may be inadequate to allow for effective submission and avoidance of aggression.

As most observations of dominance relationships have been made on weaned and adult pigs kept in crowded, artificial groupings,

questions still remained as to the natural development of dominance relationships between piglets. When were they developed and with whom? Did they remain stable across different activities and at different ages? What factors affected the dominance status acquired by an individual relative to that of other group members? Observations in the Pig Park were aimed at answering these questions.

Nearest neighbours

In the previous study by Hutton (1979), membership in sub-groups, including all animals within six metres of another member of the group, was used as a measure of the strength of social relationships between individuals. Juveniles from the same litter were found together in sub-groups more often than with non-littermates. Juveniles were more likely to stay together with other juveniles than with older group members. The adults tended to stay together, as did a pair of sub-adults who had recently reached puberty. However, the use of an arbitrary distance to define sub-group membership was a problem in that animals at either end of a long, spread-out sub-group were linked although they may not have been particularly aware of each other's presence. Therefore, frequent sampling of the identity of a piglet's nearest neighbour, regardless of distance, was used here to determine whether or not piglets stayed relatively close to particular individuals.

Social interactions and overall social relationships

Apart from agonistic interactions at and away from the udder, very little has been written about the social interactions and social relationships of piglets. Whatson and Bertram (1983)

reported that naso-nasal contacts between a sow and her young were frequent in the first five minutes after a successful suckling and suggested that this behaviour acted to re-establish the identity of the piglets nursed by the sow at a time when the sow was placid and receptive. Meese and Baldwin (1975) found that sows in farrowing crates either attacked strange piglets or examined them vigorously with their snout, while sows with their olfactory bulbs removed showed no aggression towards them. Therefore an olfactory component was implicated in the mother's recognition of her young. It was of interest to determine how mothers, other adults and juveniles in the Pig Park would react to piglets and *vice versa*.

It was also of importance to determine when different social behaviour patterns appeared in the repertoire of young piglets and to plot changes in their frequencies with age. To whom were different types of social behaviour directed, and what factors determined preferences for particular individuals? Did piglets vary in their overall attractiveness or propensity to interact with others? Did piglets develop strong and lasting social relationships with certain other individuals?

Finally, it was of interest to determine whether differences in behaviour were related to future sexual dimorphism of behaviour. For example, did males play-fight preferentially with males, and to a greater extent than females, as they would as adults? Did males perform more mounting than females? Differences in the agonistic behaviour of young males and females in other polygamous mammalian species have been related to the greater importance of combat skills in adult males (e.g., Biben, 1982).

Play behaviour

Loizos (1966) listed features which could be used to distinguish play from non-playful activities. Sequences of behaviour patterns could be reordered, and individual movements might be incomplete, exaggerated and/or repeated more frequently than they would be in non-play. Sequences could also be fragmented by the introduction of irrelevant activities or terminated before a goal was reached. Play was said to occur when an animal's primary needs (for food, rest, warmth, avoidance of predators, etc.) were satisfied, and was most common in young animals in the care of adult conspecifics. Lorenz (1981) has suggested that there is a unitary motivation for play, because animals perform rapid sequences of functionally unrelated behaviour patterns. Further defining characteristics of play include the occurrence of play signals important in the initiation of play (Bekoff, 1974), the absence or infrequent occurrence of certain aggressive and sexual acts such as threat, submission and heat standing (Rheinhardt and Rheinhardt, 1982), and the occurrence of rôle reversals and self-handicapping (Poole, 1966). Play in the Pig Park was examined to determine whether these definitions apply to piglets. The frequency and sequencing of behaviour patterns occurring in association with play markers (Chalmers and Locke-Haydon, 1981) was compared with that occurring in the absence of play markers.

Many overlapping suggestions have been made as to the possible functions of play. (See reviews by Smith, 1978; Bekoff and Byers, 1981.) Current theories generally fall into two overlapping categories, motor training and social bonding. The motor training theory includes the suggestion that play in young mammals promotes

the physiological development of muscles, bones and blood capacity (Brownlee, 1954; Fagen, 1976). For example, in mountain sheep, Geist (1971) has suggested that lambs which fail to play may develop weak skeletons and suffer broken ones more frequently as adults. Play may also provide an opportunity for the practice and learning of the complex sequences of movements involved in social encounters, escape from predators and prey capture, thereby promoting neural development and increasing the efficiency and coordination of these movements (Eibl-Eibesfeldt, 1967; Welker, 1971; Owens, 1972; Berger, 1979). In the social bonding theory, it is suggested that during play, social bonds are formed, strengthened and maintained (Baldwin and Baldwin, 1974; Poirier and Smith, 1974). Therefore, the play of piglets was examined with regard to its possible functions.

METHODS

The Pig Park

The Pig Park consists of two fenced enclosures, the gorse enclosure and the forest enclosure, measuring 1.16 and 1.14 hectares, respectively, situated on a north-easterly facing slope behind the Edinburgh School of Agriculture Pig Unit, Easter Howgate, Midlothian, Scotland. Both enclosures contain a running stream, open grassed areas, gorse-covered areas (*Ulex europeaus*) and a small bog with rushes (*Juncus sp.*). In addition, the forest enclosure includes a stand of pine trees (*Pinus sylvestris*).

The pigs

The subjects of the study were the piglets born in the Pig Park in February, June, July and August, 1980. Each was individually identified by means of coloured ear tags. The animals are referred to by symbols, with capital letters indicating adults and juveniles, and small letters representing piglets. Piglets become juveniles after natural weaning between two and three months of age and juveniles reach adulthood by eleven months of age, when they are both physiologically and behaviourally competent to reproduce.

Table 1.1 shows the composition of the pig group in the forest enclosure on 11 February 1980. Within this group, two sub-groups were recognizable from their resting behaviour. The members of the gorse enclosure sub-group and the forest enclosure sub-group had been living separately in their respective enclosures for over six months when they were both shut into the forest enclosure. However, they were still resting in separate nests two months later, when this study began.

Prior to the mixing of the two groups, a number of animals had

Table 1.1 Composition of the Pig Group in the Forest Enclosure on 11 February 1980

Animal	Symbol	Sex (M or F)	Age	Age-Class	Sub-Group	Parity	Parentage (Mother x Father)
Boar	7	M	> 5 years	Adult	Gorse enclosure	-	from Pig Unit
Sow	4	F	2¾ years	"	"	P_2	from Pig Unit
Gilt (White Blue)	WB	F	12 months	"	"	-	4 x 7
Red	R	F	6½ months	Juvenile	"	-	4 x 11
Black Pink	BlP	M	6½ months	"	"	-	4 x 11
No tag	NT	M	7 months	"	"	-	OY x 11
Sow	2	F	2¾ years	Adult	Forest enclosure	P_4	from Pig Unit
Sow (Red Red)	RR	F	17 months	"	"	P_2	2 x 1
Sow	12	F	19 months	"	"	P_2	from Pig Unit
Pink Black	PBl	M	5½ months	Juvenile	"	-	2 x 7
Pink Blue	PB	M	"	"	"	-	"
Pink Pink	PP	F	"	"	"	-	"
Pink Red	PR	F	"	"	"	-	"
Pink White	PW	F	"	"	"	-	"
Pink Yellow	PY	F	"	"	"	-	"
Green	G	M	6 months	"	"	-	RR x 11
2's new litter		2M, 5F	0 days	Piglets	"	-	2 x 11
RR's new litter		1M, 5F	4 days	"	"	-	RR x 11
12's new litter		4M, 6F	2 days	"	"	-	12 x 11

been removed from both enclosures, including a sow (OY), a young boar (11) and some or all of the juvenile offspring of the sows 4, RR, 12 and OY. The sows 2 and 4 had been introduced to the Pig Park from the Pig Unit as juveniles in November, 1977 along with an adult boar, 1, who died after siring RR and OY. The boar 11 and sow 12 were introduced as juveniles in November, 1978 along with the adult boar 7. After February, 1979, the two boars 7 and 11 were kept in separate enclosures and mated those sows which came into oestrus while being kept in their enclosures.

The piglets

Three litters of piglets were born within four days of one another in February, 1980, to sows RR, 12 and 2. Twenty-nine piglets were born alive, of which six died within their first two days, mainly as a result of crushing. Behavioural observations were made on the surviving piglets until they were thirteen weeks old, and Table 1.2 shows their names, sexes and weights along with the number of thirty minute focal samples obtained for each animal. The juveniles were removed from the forest enclosure when the piglets were fifty to fifty-four days old and ten of the piglets were removed after observations on them were concluded. (Their weights at 151 to 153 days are shown in Table 1.2.)

The next set of observations were made on WB's first litter, born on 9 June, 1980. Of thirteen piglets born alive, only four survived, and Table 1.3 shows their names, sexes and weights and the number of focal samples made on each. Four weeks later, 12 gave birth to eight piglets, of which six died within ten days leaving two male survivors, pp and pw (see Table 1.3). Observations on

Table 1.2 Names, sexes and weights of the February-born piglets

Dam	Piglet	Symbol	Sex (M or F)	Weight (kg) at different ages (days) Age: 0	1	2	21	30-34	37-41	79-83	109-113	151-153	No. of 30 minute focal samples
2	red black	rbl	M	1.25				7.3		27.5	41.5	-	8
	red blue	rb	M	0.92				7.3		25.5	39.0	-	6
	yellow green	yg	F	1.54				9.5		27.0	38.5	-	6
	yellow red	yr	F	0.92				7.0		21.5	34.0	-	6
	yellow orange	yo	F	0.93			died 1.9						3
	yellow white	yw	F	1.32				8.0	died 8.0				3
	yellow yellow	yy	F	0.98				8.0	died 8.0				4
RR	black white	blw	M		1.50			10.0		30.5	46.5	80	8
	blue pink	bp	F		1.28			7.0		26.0	40.0	-	7
	blue red	br	F		1.38			8.5		31.0	45.0	75	7
	blue green	bg	F		1.10			7.3		24.8	37.0	-	7
	blue blue	bb	F		1.30			9.0		31.0	45.8	77	8
	blue yellow	by	F		1.26			9.3		31.3	45.0	77	8
12	white orange	wo	M			2.1		10.5		32.3	46.0	81	6
	white green	wg	M			1.9		8.5		25.5	37.5	-	6
	white black	wbl	M			2.7		9.5		30.5	44.5	76	7
	white red	wr	M			2.7		10.5	died 11.2				2
	pink yellow	py	F			1.7		9.0		32.3	48.5	82	6
	pink blue	pb	F			1.9		10.0		32.0	46.0	81	6
	pink red	pr	F			2.2		10.5		33.3	46.0	76	6
	pink black	pbl	F			2.1		11.5		36.5	55.5	89	6
	pink white	pw	F			1.9		7.5		24.0	36.0	-	6
	pink green	pg	F			1.6		9.3		28.5	41.0	-	6

Table 1.3 Names, sexes and weights of the June and July-born piglets

Parentage Dam x Sire	Piglet	Symbol	Sex (M or F)	Weight (kg) at different ages (days) Date: 9.7.80	10.6.80	20.6.80	10.7.80	29.10.80	7.11.80		No. of 30 minute focal samples
				Age: 0	1	11	3	114	123	151	
WB x 7	black pink	bp	M	1.5	1.7	-	-	-		80	16
	black orange	bo	M	1.2	1.4	-	-	-		75	16
	black brown	bb	M	1.5	1.8	died 3.5					6
	white yellow	wy	F	1.4	1.5	-	-	-		70	16
12 x 7	pink pink	pp	M				2.4	38.5	41		-
	pink white	pw	M				2.3	-	56		-

WB's piglets continued until they were six weeks old, when the nine remaining juveniles from RR's, 2's and 12's previous litters were removed from the Park.

The third group of piglets observed in the Pig Park in 1980 were the litters of RR and 2, born on 15th and 18th of August. The gates between the two enclosures had been opened a week previously, allowing the animals to enter the gorse enclosure, and the two sows had built separate farrowing nests in there. Twenty-nine piglets were born, of which five died early. Focal observations began when the piglets were four weeks old and continued until their thirteenth week. At this time, the juveniles from WB's and 12's previous litters, and the now weaned piglets of RR and 2, were removed from the Pig Park. Their weights and sexes are shown in Table 1.4, along with the number of focal samples made on the focal animals. It should be noted, that while sows 2, RR and 12 gave birth to two litters, and WB to one litter, in 1980, sow 4, who was very thin, did not produce any piglets that year.

Husbandry

The pigs were fed pelleted rations once a day at approximately 1000 h. The basic amount varied with the time of year, age and reproductive state, with lactating sows being fed additional food in a holding pen. The piglets learned to enter the holding pen through a piglet-sized entrance for creep food (about 0.2 kg per piglet) during their second week, and after this, were fed there on increasing amounts of food according to their requirements (up to 1.0 kg per piglet towards the end of the suckling period). Water was available from the streams in the Pig Park, and additional food

Table 1.4 Names, sexes and weights of the August-born piglets

Parentage Dam x Sire	Piglet	Symbol	Sex (M or F)	Weight (kg) at different ages (days) Date: 15.8.80	18.8.80	3.9.80		7.11.80		No. of 30 minute focal samples
				Age: 0	0	16	19	81	84	
2 x 7	black black	ss	M		1.64	4.95		28.5		7
	black red	sr	M		1.50	4.75		27.8		-
	black yellow	sy	M		1.00	3.50		22.0		7
	black pink	sp	M		1.14	3.90		26.5		-
	black orange	so	M		1.62	4.85		29.5		-
	orange pink	op	M		1.26	4.55		25.0		-
	orange black	os	M		1.18	4.35		13.5	14.0 died 14.11.80	-
	blue blue	bb	F		1.40	4.65		26.8		7
	blue white	bw	F		1.30	4.45		24.3		-
	blue green	bg	F		1.10	3.45		19.5		-
	blue pink	bp	F		1.44	4.65		27.0		7
	blue black	bs	F		1.70	4.85		24.3		-
	blue orange	bo	F		1.40	4.45		26.0		-
RR x 7	orange orange	oo	M	1.20			4.35		21.5	-
	orange red	or	M	1.38			4.85		27.8	-
	orange blue	ob	M	1.31			4.50		27.5	7
	orange green	og	M	0.92			4.05		22.0	7
	no tag	nt	M	1.26			4.50		26.0	-
	black green	sg	M	0.72			3.75		24.5	-
	black white	sw	M	1.16			4.05		25.3	-
	yellow yellow	yy	F	1.26			3.95		24.8	7
	yellow green	yg	F	0.70			1.45	died 10.9.80		-
	yellow pink	yp	F	1.16			3.76		25.5	-
	yellow white	yw	F	1.40			4.57		29.0	7
	yellow red	yr	F	0.96			1.60		13.5	-

(mainly providing bulk) was obtained through foraging on grass, and tree roots and bark.

Corrugated iron shelters were erected over farrowing nests, and straw was supplied to provide additional protection for the young piglets. Straw was also provided to the other nests during cold weather. After farrowing, the piglets were weighed and individually marked with ear tags. Teeth, tails and testicles were left intact. Adults were wormed yearly, and medical problems were dealt with by a veterinarian. Daily weather records were kept, and Appendix A gives information about the temperature, rainfall and wind in 1980.

Methods of observation and analysis

I The ethogram

Preliminary observations were carried out upon piglets kept extensively in the Pig Park and intensively in farrowing crates and pens during the autumn of 1979. From these observations, a detailed ethogram of behaviour patterns was devised for piglets, which was used in subsequent investigations in the Pig Park.

II Suckling behaviour

The following information was recorded:

1 Time of day, identity of the sow and location in the Pig Park.

2 Suckling position of the sow (lying on her right side or left side, standing or sitting)

3 Teats used by each piglet. Teats were numbered from the anterior to the posterior end of the udder and prefixed with an L (left) or an R (right) to denote the side of the udder on which they were situated. If the sow normally lay on her left

side to suckle, the left row of teats was considered to be the lower row and the right row was the upper row.

4 Participants in fights for teats.

5 Identity and behaviour of pigs, and piglets from other litters, which sniffed at the udder, suckled, or disrupted a suckling bout in some way.

6 Initiator(s) and terminator(s) of a suckling bout, where evident.

7 Whether the suckling occurred with or without milk let-down.

8 Aggressive behaviour directed by the sow towards piglets attempting to suckle from her.

Not all the above information was obtained for all suckling bouts. Analysis involved an examination of the time intervals between suckling bouts with and without milk let-down, and the frequency and synchronization of suckling by different litters of piglets. The positions and changes in position of piglets in the teat order was related to their weight and growth rate.

III Resting behaviour

At thirty minute intervals, scan samples were made of the identities of all animals resting together in each nest. An animal could be resting alone or with any number of other pigs up to a maximum of the entire group. The identities of individuals lying in contact with one another versus further apart in a resting group (huddle) were not distinguished because previous observations had shown that considerable movement occurred during resting bouts, and animals resting together at any one time may have only been in contact because others between them had moved or because one had moved while the other was sleeping. Therefore, individuals were not

necessarily concerned about the identities of their nearest neighbours while resting. Also, Kuipers and Whatson (1979) observed no obvious selection of resting neighbours in piglets.

The data obtained on resting group membership was analysed using cluster analysis to determine the relative probability of each piglet resting with each other member of the group. The following cluster analysis technique is described by Morgan *et al.* (1976). A Dice similarity was obtained for each dyad in a group by dividing the number of scans in which each pair of pigs was resting together in the same nest by the sum of the total number of scans in which each member of the pair was observed resting. The result was multiplied by 1000 to give a whole number. The similarities were then used to construct dendrograms, which were used to illustrate the changing resting relationships of piglets during their development. Dendrograms were formed by linking each animal to the animal with which it was most similar. Individuals with high similarity values were linked on the dendrogram at a low level, and those with lower similarities were joined in at increasingly higher levels.

A problem with using dendrograms is that, through a process of 'chaining', a sub-group of animals (a cluster) could be linked on a dendrogram at a particular level of similarity although each member was actually only similar to one other member of that cluster. In order to determine whether clusters on the dendrogram formed well-knit groups, B_2 cluster analysis was performed (Jardine and Sibson, 1968). A B_2 cluster consisted of a group of animals all linked to at least two other members of the group by similarities greater than, or equal to, the similarity connecting them on a dendrogram.

IV Social facilitation

Active piglets were followed for thirty minute periods in pre-determined order and a record was kept of the identities of all animals within ten metres which performed bouts of (a) rubbing and scratching the body, (b) drinking water, (c) sniffing at the observer and (d) sniffing at unusual objects (e.g. an empty crisp bag, a piece of baler twine, plastic pipes, a dead slug, a dead mouse) which were occasionally found in the Pig Park. These activities were chosen because they were relatively uncommon and appeared highly emulative. A timer marked thirty second intervals during inter-individual sequences of these activities. A triangular matrix was drawn up to show the number of times which each pair of animals in the group performed one of the activities in an inter-individual bout. A bout of a particular behaviour was considered to have begun when an animal performed that behaviour and to have ended when the behaviour was not performed by any animal in the vicinity for at least three minutes after the last occurrence. This definition was based on previous work done by the author (Hutton, 1979). For each pair of animals participating in a bout, a score of one was added to their cell in the matrix, regardless of the number of times which they performed the activity during that bout. The Dice similarities were calculated for each pair after combining the data from the four types of inter-individual bout. The animal(s) with whom each piglet was most similar was determined, and, as before, at the similarity level at which all piglets were connected in one group, B_2 cluster analysis was performed. Appendix F gives additional information on the sampling method and sample sizes.

V Dominance relationships

A record was kept of all agonistic encounters observed while in

the Pig Park. The identities of the interactants were noted, along with the type and intensity of the interaction and its outcome. Dominance was based on observations of avoidance occurring away from the udder and while participating in activities other than feeding on creep food (an artificial situation) and mounting (which almost always resulted in avoidance). If an animal made an obvious movement away from the close vicinity of another (i.e. within one metre) immediately after the approach of, or interaction with, that animal, then it was considered to have avoided the other animal. Matrices were drawn up showing the number of times which each pig avoided each other member of its group. To determine whether the results indicated the presence of a dominance hierarchy, attempts were made to arrange the piglets in the matrix so that most of the scores fell above the diagonal. Dominance relationships apparent on the matrix were compared with the direction of avoidance occurring at the udder, while feeding at the feeding site and after mounting.

VI Focal animal samples

Sampling methods

The continuous sequence of behaviour performed by the focal animal over a thirty minute period was recorded on a small portable tape recorder. During the sample, a battery operated timer 'beeped' at thirty second intervals, providing a time scale. For each sample, the following information was transcribed in number-coded form on to Data Preparation Sheets for entry into the computer.

1 The name and age of the focal piglet and the time at which sampling commenced.

2 The sequence of behaviour patterns performed by the piglet,

divided into thirty second intervals by time markers. Social behaviour patterns were followed by the name of the animal interacted with. A behaviour pattern could not be followed by itself.

Thus, information was gained on behavioural frequencies and sequences, and on social interactions. Nearest neighbour information was also obtained by recording the identity and occupation of the nearest neighbour of the focal animal at five minute intervals throughout the sample. Where several animals were close by, the one with its head closest to the focal animal was considered to be the nearest neighbour. It was felt that communication and awareness of each other's identity was most likely to occur between animals with their heads close together.

Focal observations were made on all piglets in the February and June litters, and on eight piglets (four male and four female) in the August litters. Attempts were made to obtain an equal number of samples for each piglet by observing each one in the group in a predetermined order before moving on to the next set of observations. A new random order was used in each run through the animals so as to obtain observations on each piglet at different times of day. Two to six focal samples were made each day between 0900 hours and 1700 hours, with the majority falling between 1100 and 1500 hours (i.e. after the morning feed and before the light faded in the evening). Sampling began when the focal animal had resumed its current activity after noting the presence of the observer, and care was taken to avoid startling or disturbing the piglets. Refer to Appendix F for a breakdown of the number of focal animal samples made on each litter during each age period and the number of animals contributing to the sample size.

Frequency analysis

Analysis was done on the Edinburgh University computer system using Fortran and Imp programs written by the author (unless otherwise stated). In order to obtain mean frequencies for each behaviour pattern (in terms of the number of times per thirty minute focal sample), the data was lumped into the following age groups: 1-8; 9-17; 18-27; 28-41; 42-55; 56-69; 70-91 days of age. The total number of occurrences of each behaviour at each age was divided by the total number of focal samples made at that age. The minimum and maximum number of times that a behaviour occurred during a focal sample at that age provided its frequency range.

Some behaviour patterns were of long duration without interruption (e.g. lying on the belly), and therefore had a low mean frequency. In order to give an indication of the time spent in these activities, the mean, minimum and maximum number of thirty second time intervals, in which each behaviour occurred over a thirty minute period, were also obtained from the data.

Comparisons of the behavioural frequencies of different individuals or groups were made using the chi-squared test (Siegel, 1956), based on the assumption that if two values belonged to the same population , then each would not differ significantly from their mean.

Sequence analysis

The sequence of behaviour occurring in the focal samples was entered into a preceder-follower matrix, showing the number of times which each behaviour pattern was immediately followed by each other behaviour pattern. In order to determine which behavioural

transitions occurred more often than would be expected by chance, a matrix of expected values was generated using a computer program modified for use on the present data from one written by Slater and Ollason (1972) and converted from Algol to Imp by J. Deag (Department of Zoology, University of Edinburgh). The program used row and column totals from the 'observed' matrix to produce values which would be expected if differences in the frequencies of behavioural transitions depended only on the relative level of occurrence of each behaviour. A process of iteration produced values of zero for the diagonal cells of the 'expected' matrix, as transitions between a behaviour and itself could not occur. Each observed value was then compared with its expected value, and providing that the expected value was greater than five, the chi-squared test of significance, with one degree of freedom, was performed. Sequence analysis was used to describe changes in behaviour with age and to compare playful and non-playful sequences of behaviour.
(See Appendix F for more detail of the procedure adopted.)

Analysis of social interactions

Social interactions were analysed using the Statistical Package for the Social Sciences (SPSS). The number of times which each focal piglet interacted with each other animal in the Pig Park was determined, distinguishing between the different social behaviour patterns described in the ethogram. The number of times which each piglet interacted with its dam, another sow, the boar, a juvenile, or a male or female littermate or non-littermate was determined for different age groups, and cluster analysis was performed to find out whether certain animals were preferred for certain types of social interaction at certain ages.

Nearest neighbour analysis

For the purpose of analysis, only nearest neighbours recorded during periods of activity were counted. Those recorded during suckling and resting were discarded as many animals were in close contact at these times and it was often difficult to distinguish a nearest neighbour. During resting, two animals could remain nearest neighbours over several scans, even though others were also in close contact, and while suckling, the nearest neighbours were those piglets which were adjacent in the teat order, which were likely to be the same at every suckling. The remaining data was entered on an inter-individual matrix and subjected to cluster analysis. The results are presented in the form of maximum spanning trees (Morgan *et al.*, 1976), whereby each piglet is connected to the animal with whom it is most similar. B_2 clusters are also illustrated by means of dotted lines around the animals in each cluster.

Analysis of play behaviour

Play behaviour was analysed in the following manner. Behaviour patterns which always appeared playful to the observer were designated as 'play markers', after Chalmers and Locke-Haydon (1981). It was assumed that behaviour occurring in association with play markers was also performed in a playful context. The behaviour patterns used as play markers were scampering, hopping, pivoting, tossing the head, flopping, shaking objects and bumping into other piglets. A frequency histogram was drawn, plotting the number of thirty second intervals which elapsed between successive performances of play markers, and this showed that the majority of

play markers occurred within two intervals of each other. Therefore, a play bout was defined as 'the sequence of behaviour patterns occurring in a series of thirty second intervals, in which a play marker appeared in at least one out of every two consecutive intervals'. All other behaviour was considered to be non-play. It was then possible to compare the frequency and sequencing of behaviour patterns occurring in play versus non-play bouts at different ages. The play sequences of males versus females were also compared.

RESULTS

I The ethogram

An ethogram of ninety-two piglet behaviour patterns observed in the Pig Park is presented for reference in Appendix B.1. The behaviour patterns were in many cases similar or identical to those described for adult European wild boar (Frädich, 1974; Beuerle, 1975) and for adult domestic pigs in the Pig Park (Stolba, 1979). However, aspects of nest building (carrying nesting material to the nest), marking (stroking the antorbital region and chin against branches), sexual behaviour (champing jaws, court grunting, copulation, heat standing) and fighting behaviour (deep throated grunts, biting with tusks, salivation while fighting) had not yet appeared. In addition, some behaviour patterns were performed only by piglets (suckling behaviour, crawling on the belly, squeaking).

The piglet ethogram was used to describe the sequence of behaviour patterns performed during focal animal samples. Changes in the mean frequencies and sequential ordering of these behaviour patterns during development are described in the ensuing sections. For reference, a complete list of mean frequencies (in terms of the mean number of times which a behaviour pattern was performed per 30 minute focal sample, and the mean number of 30 second intervals in which the behaviour occurred per 30 minutes) along with ranges, is provided in Appendix B.2 for each age period.

A number of problems with the ethogram arose during the course of the investigations. Most of the behaviour patterns were easily identified. However, the consistency with which scampering was distinguished from galloping, and whining from squeaking were

questionable. Also, some behaviour patterns varied in form at different ages and/or in different contexts. These differences would have provided interesting additional information about the behavioural development of piglets, but were included within broad behavioural categories because they changed along a perceptual continuum rather than forming discrete units of behaviour.

As behaviour patterns often followed one another in quick succession, it was necessary to make instant decisions about the classification of each movement. A more detailed analysis could have been accomplished by filming the behaviour and playing it back. By measuring the exact durations, frequencies and intensities of the components, strict criteria could have been used to sub-divide behaviour into smaller units. Video recording was attempted in the Pig Park, but proved impractical due to difficulty in following a rapidly moving piglet through the undergrowth with heavy equipment.

The ethogram was split into as many categories as possible to allow for comparisons between different ages and environments. Behaviour rare at one age or in one environment took on greater significance at later ages and in different situations. However, some of the behaviour patterns distinguished proved redundant. For example, rubbing of the head was recorded separately to rubbing the body as it was thought that it might indicate the onset of marking behaviour. However, as it was uncommon, and did not involve wiping of the antorbital region against objects, it could be lumped with rubbing of the body in future analyses of piglet behaviour. Lumping of behaviour patterns would not be justified in many other cases, as they occurred in different contexts and had different sequential contingencies. For example, sniffing at the head often

involved an investigatory and/or agonistic component, whereas sniffing at the body usually occurred during huddle formation, when passing others and while resting in contact.

Frequency analysis showed that most behaviour patterns appeared within the first eight days of life, indicating that the piglet is born in a fairly advanced state of physical development when compared with highly altricial animals such as mice. However, if behaviour patterns had been distinguished on the basis of characteristics such as balance, sure-footedness, strength and awareness, the immaturity of the young piglet would have been stressed. Where infantile behaviour patterns were recorded (e.g. crawl on belly, squeak) their frequencies declined to zero from initially high levels.

It is obvious that problems of classification arise during the study of behavioural development (Hinde, 1971). Hopefully the frequencies and sequential dependencies of the different behaviour patterns described in this study will provide a basis for future research. More detailed methods of examining changes in motor action patterns during development are described by Fentress (1981) and Golani (1976).

II Suckling behaviour

1 Frequency changes with age

Figures 1.1 and 1.2 illustrate the mean frequencies of various suckling behaviour patterns at different ages. The time spent sucking and massaging at the piglet's preferred teat decreased with age during the first month, increased during the second month and decreased further during the third month. At birth, the sow spent

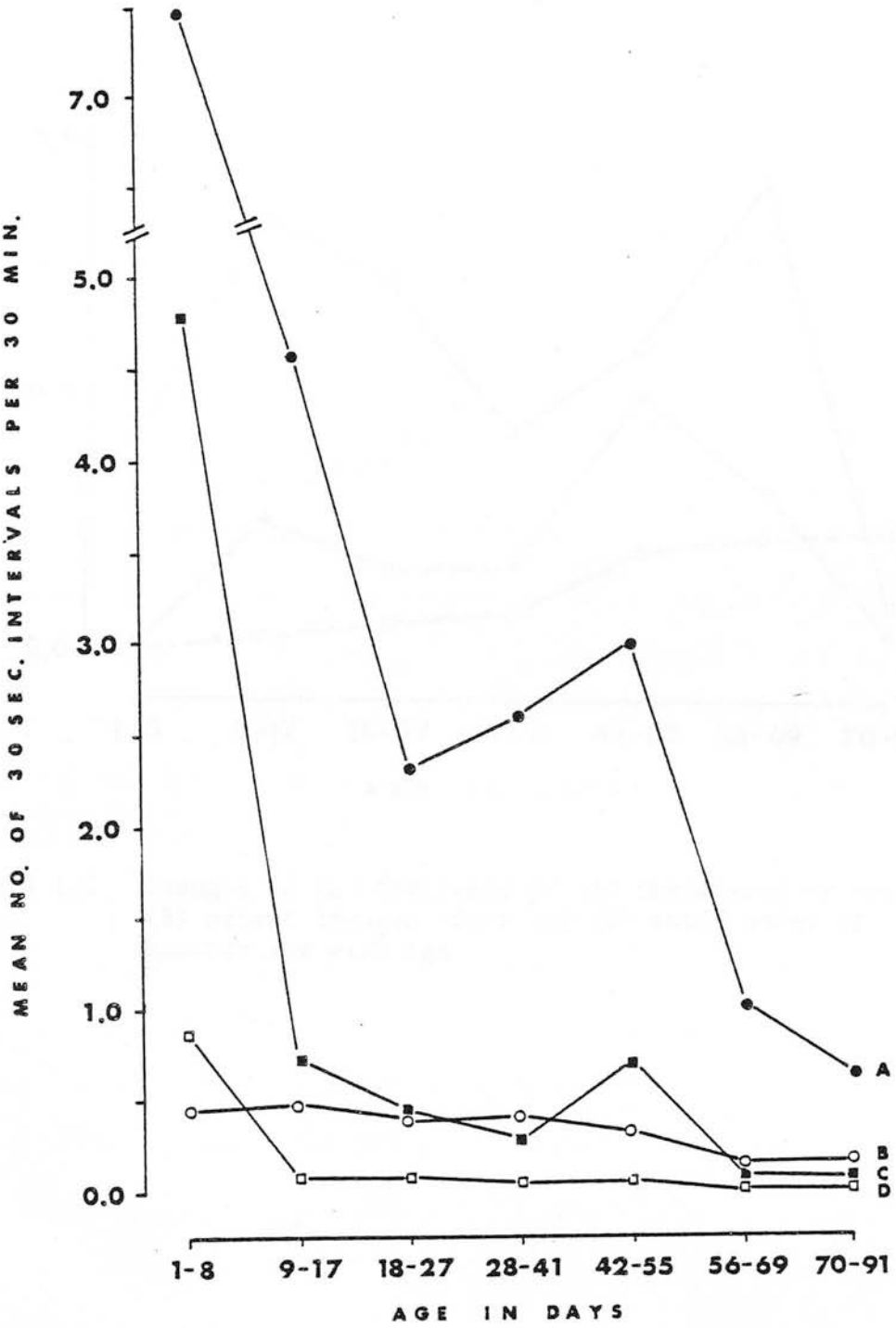

Figure 1.1 Changes in the number of intervals in which (A) suck teat, (B) drink milk, (C) sniff udder and (D) fight for teat occurred with age

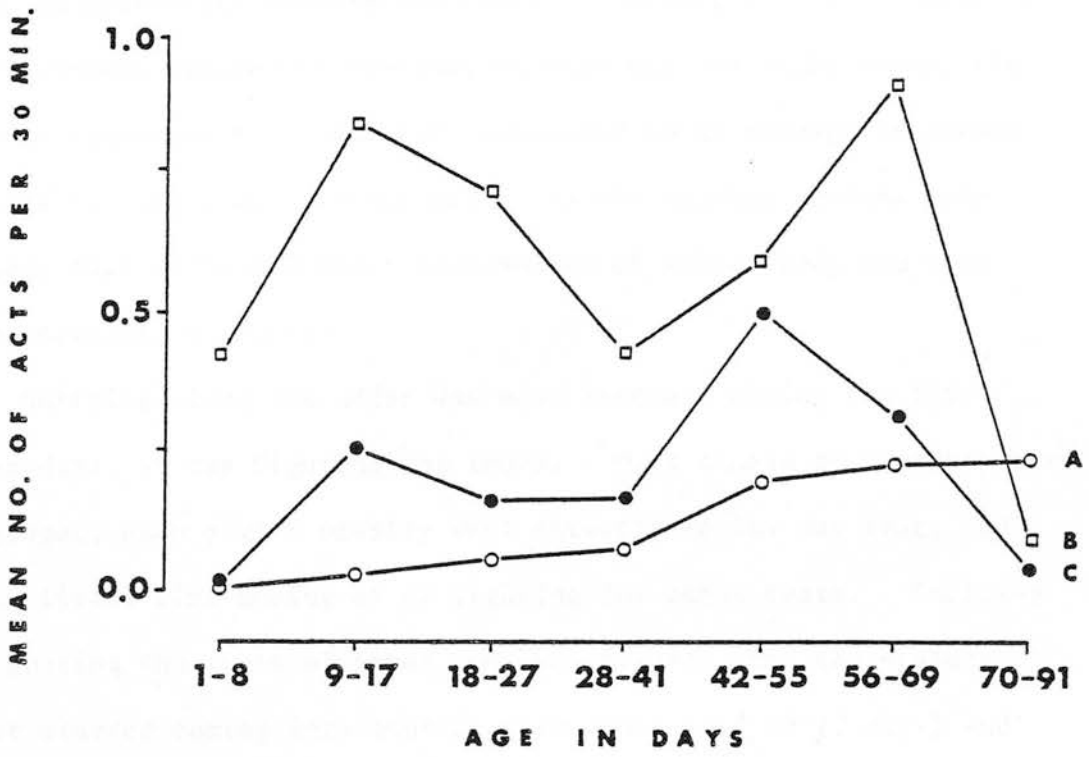

Figure 1.2 Changes in the frequency of (A) threatened by sow, (B) orient towards udder and (C) sniff udder of another sow with age

long periods lying on her side in the farrowing nest, exposing her teats to her piglets, but as the piglets grew older, more time was spent in activities outside the nest. However, as the frequency of milk let-down started to decline, between six and eight weeks, the piglets increased their suckling behaviour in an attempt to induce the sow to suckle more frequently. As the weaning process continued, they increased their consumption of solid food, and made fewer attempts to suckle.

Sniffing along the udder was most frequent during the first eight days, as was fighting for teats. Once stable teat orders were developed, each piglet usually went directly to its own teat, and spent little time nosing at or fighting for other teats. Sniffing and sucking the teats of other sows was highest when the piglets first started coming into contact with other sows (9-17 days) and also between 42 and 55 days. These periods coincided with the switching of mothers by two piglets.

While out of the nest, the piglets would follow their mother closely as she walked, stretching their mouths towards their teats, and taking hold of them as soon as she stopped. This behaviour was most common between nine and seventeen days of age, when they remained close to their mother, and also between eight and ten weeks, when they were hungry for milk during weaning. At this time, fewer actual contacts were made with the udder, as the sow either walked away, or swung her neck around and snapped and growled at them (i.e. threatened them).

Both rapidly and slowly repeated grunting (Figure 1.3) peaked at the age of eight to ten weeks, which coincided with the weaning period. Slowly repeated grunts were mainly given during locomotion

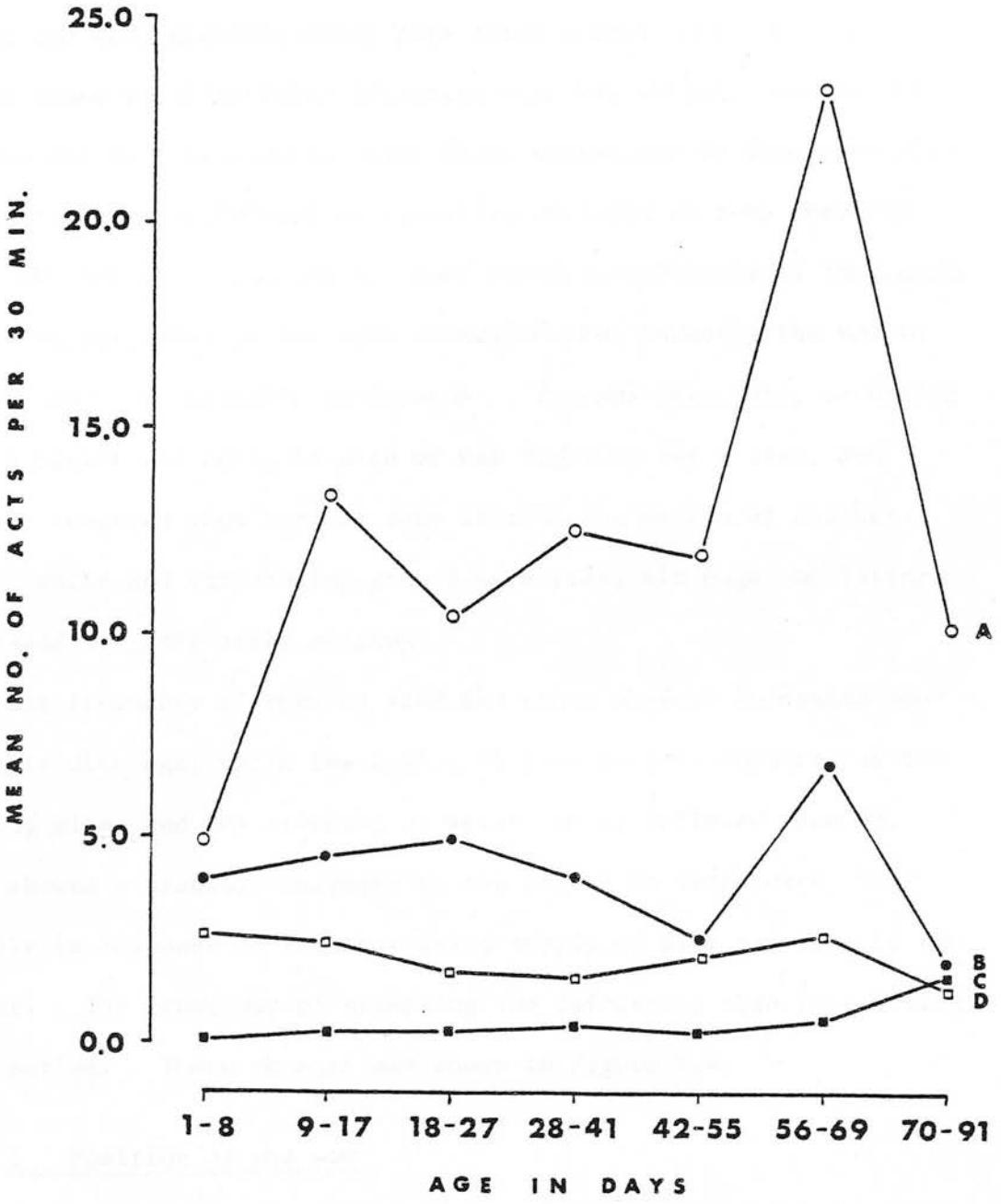

Figure 1.3 Changes in the frequency of (A) slow grunting, (B) rapid grunting, (C) threatening grunts and barks and (D) whines, squeaks, squeals and screams with age

and foraging, while rapid grunting was performed when separated from others and when greeting other pigs after a period of separation. High-pitched vocalizations, including squeaks, whines, squeals and screams did not, as a whole, show large variations in frequency with age, but, taken individually, squeaking declined to zero over the first two months as whining (a lower pitched vocalization) increased. Both were performed in the same context - when inducing the sow to suckle, and were probably synonymous. Screams were rare, occurring when a piglet was being handled or was fighting for a teat, and squeals occurred when running away after being bitten by another pig. Barks and threatening grunts were rare, although the latter increased slightly after weaning.

The frequency of chewing food and other objects increased continually with age, while the eating of food pellets supplied at the feeding site, and the drinking of water, which followed feeding, both showed a dramatic increase in the eighth to tenth week, presumably in response to the decreasing supply of milk provided by the mother. The frequency of urinating and defecating also rose during this period. These changes are shown in Figure 1.4.

2 Position of the sow

Table 1.5 shows the number of occasions on which each sow was observed to suckle while (a) lying on her left side, (b) lying on her right side, (c) standing, or (d) sitting. Most of the sucklings with milk let-down occurred while the sow was in her normal suckling position. It appears that the sows tended to suckle successive litters in the same position, with RR on her left side, 12 on her right side and 2 standing.

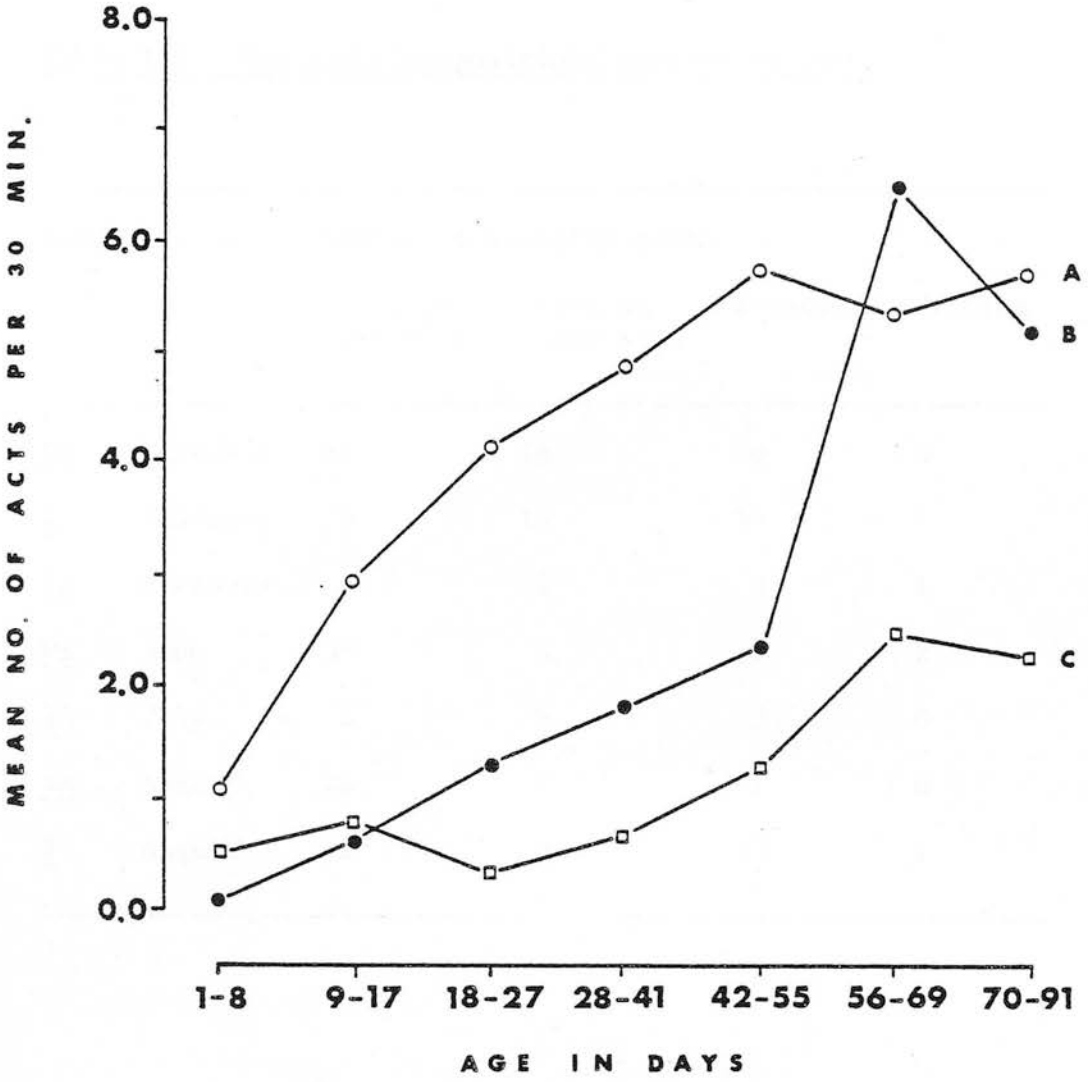

Figure 1.4 Changes in the frequency of (A) chew, (B) eat food, drink water and (C) urinate, defecate with age

Table 1.5 The suckling positions adopted by each sow

Sow	Litter	Number of suckling bouts			
		Lying on left side	Lying on right side	Standing	Sitting
RR	February	81	16	0	0
2	February	23	14	35	1
12	February	5	57	0	1
WB	June	38	5	9	2
12	July	2	9	3	0
RR	August	28	1	1	0
2	August	2	9	23	1

Sow 2 first stood to suckle her February-born piglets when they were nine days old, but the piglets had trouble reaching the udder, and she only regularly stood to suckle after they were one month old (see Plate 2). By this time, they were relatively large, and crowded the udder when she suckled lying on her side, requiring all piglets to reach for their teats from one side. When she stood, the piglets could approach their teats from either side. The same applied to her August litter, which she regularly suckled in a standing position after they were twenty-five days old.

Sow WB first stood to suckle her piglets when they were eight days old, but they could not reach their teats properly and she did not let down milk. The first successful upright suckling occurred the next day, and WB often stood to suckle during periods of activity (i.e. away from the nest) after the piglets were fifteen days old.

3 Piglet growth rates

Table 1.6 compares the growth rates of piglets suckling from the upper (e.g. right row of teats if the sow normally lay on her left side) anterior four teats, lower anterior four teats, upper posterior three teats and lower posterior three teats over various age periods. (It is unfortunate that more frequent and regular weighings of piglets were not obtained. However, after the piglets were two to three days old, they were very difficult to catch, and for up to five days after a weighing session, they could not be observed properly because they kept running away out of sight. Handling of piglets also upset their mothers, who tended to remain wary of, and aggressive towards the observer for several days.) It

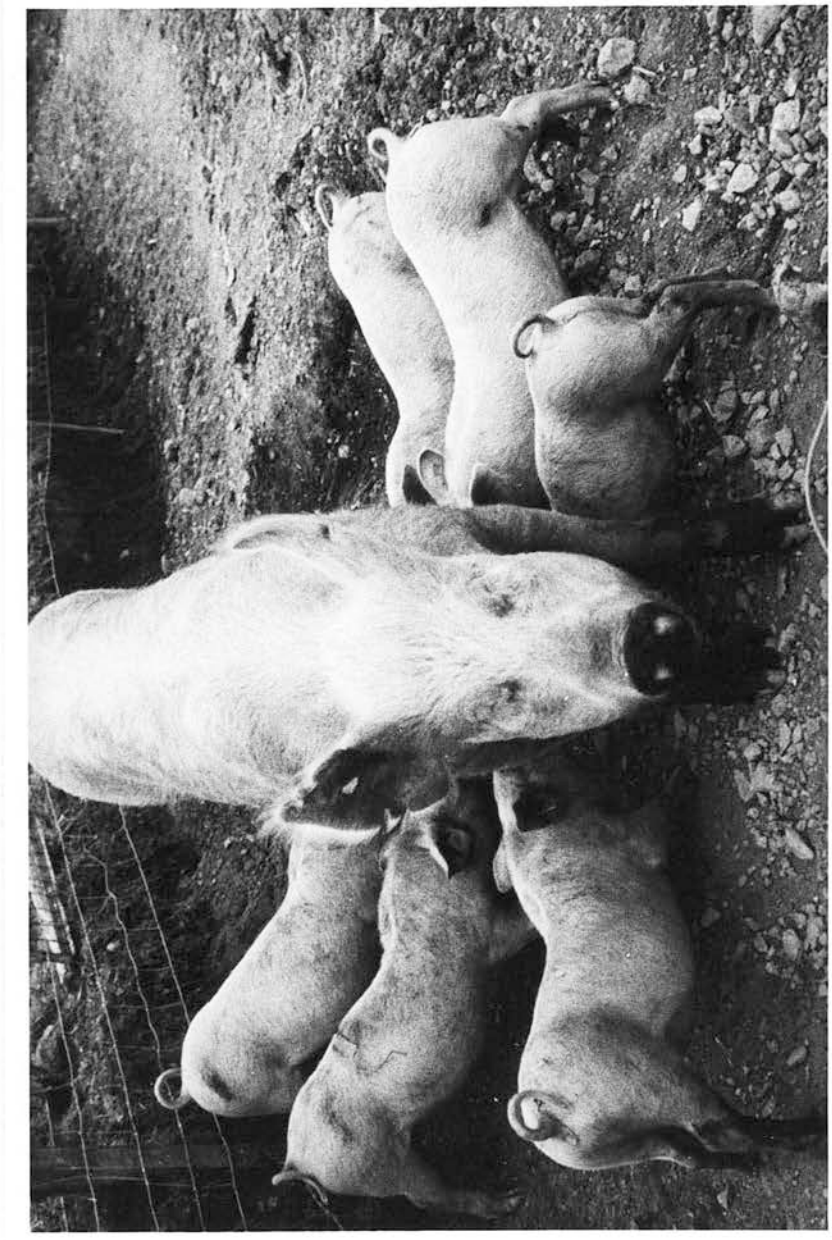

Plate 2 Sow 2 stands suckling her nine week old piglets at the feeding site in the forest enclosure

Table 1.6 Piglet growth rates in relation to the positions of their teats

Sow	Litter	Age period (days)	Overall mean weight gain per piglet (kg)		Mean weight gain per piglet (kg)							
					Upper 4 Anterior teats		Lower 4 Anterior teats		Upper 3 Posterior teats		Lower 3 Posterior teats	
			$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n
RR	February	1- 34	6.9	5	6.6	2	5.7	1	8.0	1	7.7	1
		34- 83	20.6	5	20.0	2	19.0	1	22.0	1	22.0	1
		83-113	13.7	5	13.1	2	14.0	1	13.7	1	14.8	1
2	February	0- 30	7.0	7	6.8	4	7.2	3	-	0	-	0
		30- 79	19.2	6	18.9	4	19.6	2	-	0	-	0
		79-109	14.0	6	13.6	4	14.8	2	-	0	-	0
12	February	2- 32	7.6	10	8.4	4	7.5	4	6.6	1	5.6	1
		32- 81	20.7	8	22.9	4	19.8	3	17.0	1	-	0
		81-111	13.7	8	14.9	4	12.8	3	12.0	1	-	0
WB	June	0- 1	0.2	4	0.2	2	0.2	1	0.3	1	-	0
		1-151	73.5	3	73.4	2	73.6	1	-	0	-	0
12	July	3-123	46.2	2	38.6	1	-	0	53.7	1	-	0
RR	August	0- 19	3.0	12	1.8	4	3.0	3	3.1	3	3.2	2
		19- 84	20.2	11	19.8	3	20.0	3	20.3	3	22.3	2
2	August	0- 16	3.1	13	3.0	4	3.2	4	3.2	3	2.6	2
		16- 81	20.2	13	20.3	4	19.0	4	22.5	3	19.3	2

is evident that growth rates were not affected by teat position in any consistent manner. For example, in both of RR's litters, piglets suckling from posterior teats grew slightly faster than those at more anterior teats. In 12's Spring litter, piglets at anterior teats were the more rapid gainers but in her July litter, the piglet suckling from a posterior teat gained more weight than the one suckling from an anterior teat. There was very little difference overall between the growth rates of piglets on upper versus lower row teats. However, it is interesting that, in general, piglets were more likely to be found suckling from anterior rather than posterior teats, and from upper rather than lower teats, even though, once they had chosen a teat at any position along the udder, they were likely to grow at the same rate. Also, there was a tendency for piglets from posterior teats to suckle at more anterior ones during the absence of their normal owners.

4 Teat orders

Table 1.7 illustrates the teat order of each litter at different ages during development.

RR's February litter

Within three days, RR's February-born piglets were suckling consistently from certain teats. Piglets bp, blw, bb and by sucked L1, L3, L5 and R6, respectively, while piglet br switched rapidly between R1, 2, 3 and 4, and bg switched between R3, 4 and 5. (Teat L2 was a small and probably non-functional teat, and was not used by either of RR's litters, as was R6 on 2's udder.)

When twelve days old, RR's piglets started to rest and suckle in 2's farrowing nest along with 2 and her litter. Two days later,

Table 1.7 Teat orders

Sow	Litter	Age (days)	Teat most preferred by each piglet														
			Left row of teats							Right row of teats							
			L1	L2	L3	L4	L5	L6	L7	R1	R2	R3	R4	R5	R6	R7
RR	February	3	bp		blw		bb					br	bg		by	
		16	bp				bb				br	bg		by		
2	February	3	yw	rb	yo[a]					yg	yr	rbl	yy			
		10	yw[a]	blw[b]	rb					yg	yr	rbl	yy[a]			
		46		blw	rb					yg	yr	rbl	py[b]			
12	February	4	pbl	wr[a]	pb	pr	wg			wbl	py	wo	pg	pw		
		48	pbl	wo	pb	pr	wg			wbl		pw	pg			
WB	June	2	bp							bo			wy	bb		
		7	bo							bp			wy	bb[a]		
		11	bo							bp			wy			
12	July	3[c]	+	+	+	+	pw	pp		+	+					
		10	pp				pw									
RR	August	14	sw		sg	og	ob	nt		yr	yg[a]	yw	yp	yy	or	oo
		27	sw		sg	og	ob	nt		yr		yw	yp	yy	or	oo
2	August	11	ss	sy	bw	bs	bp	so	op	sr	os	bb	bo	sp		bg

[a] yo, yw, yy, wr, bb and yg died during the course of observations

[b] blw and py started suckling from 2 after suckling originally from their mothers RR and 12 respectively

[c] piglets which died within their first ten days are denoted by the symbol +

RR's piglet blw began to suckle from 2's teat, L2, rather than from his own. In blw's absence, br suckled from his unoccupied teat as well as from her own, but within the next two days, it had started to regress along with other less used teats and after this, br consistently obtained milk from R2, bg from R3 and bb from R5. (Although they continued to suck rapidly at other teats, they probably got little or no milk from them.)

After RR's piglets were six weeks old, they tended to miss some sucklings. However, on only one occasion (at forty-six days of age) was a piglet from another litter observed to suckle from one of their teats. She was 2's piglet, yg, and she sucked by's teat, despite receiving knocks from bg during the absence of by and bb from a suckling.

2's February litter

On their second day, preferences were shown by 2's piglets yg, yr, rbl, yy and yw for teats R1, R2, R3, R4 and L1, respectively, while yo and rb fought at the udder for possession of teat L2. However, by the next day, rb was sucking peacefully from L2 while yo used L3. This teat order remained stable until the intrusion of blw from RR's litter when the piglets were ten days old. After this, blw suckled L2, presumably after fighting successfully to take it from rb. Piglet rb then dislodged yo from her teat and consistently suckled L3 thereafter, leaving yo without a productive teat. Over the next week, yo was observed to suckle on one occasion from yr's teat while yr suckled from rbl's teat and rbl fought unsuccessfully for rb's teat. After this, yo was unable to dislodge others from their teats and, as she grew thinner and

weaker, she sucked at the small, dry posterior teats and did not attempt to fight for a productive teat. She died twelve days after losing her teat. A comparison of her behaviour with that of blw, who had ultimately caused her death, showed that she performed significantly more walking, rapid grunting and lying in contact than blw, who sniffed the ground, rooted, played, sniffed and bit other piglets, and received more bites than she did.

After yo's death, the teat order remained stable until the deaths of yw and yy during their sixth week. At this time, blw started to suck yw's unoccupied teat as well as his own. Also, 12's piglets began pushing in at the posterior end of 2's udder during suckling bouts, and although rbl knocked at these piglets and defended his own teat, he did not prevent 12's piglet, py, from taking over yy's teat. Over the next three days, py was able to obtain several extra feeds from yy's teat, and to defend it from her littermates (who sucked at the dry posterior teats) while continuing to suckle from her own teat on 12's udder. However, after this, although she continued to push in at 12's udder for another week, she obtained milk only from 2.

12's February litter

In this litter, a stable teat order was apparent within four days of birth, with pbl, wr, pb, pr and wg suckling from L1 to L5, and wbl, py, wo, pg and pw suckling from R1 to R5. This did not change until their sixth week, when wr died and py switched to 2's udder, leaving two vacant productive teats. Piglet wo then switched to wr's teat, and pw moved to wo's teat. However, from this time onwards, some piglets frequently missed sucklings,

because they were resting or foraging in another part of the Pig Park, and in their absence, their littermates took advantage of their teats. For instance, pbl suckled from L2 as well as L1 when she got the chance, and wg was observed to suckle from L4, L5 and R4. The former teats of py (R2) and pw (R5) dried up through lack of use.

WB's litter

Within two days of birth, WB's piglets bp, bo, wy and bb preferred teats L1, R1, R4 and R5, respectively, but bp and bo had switched by the end of the first week. When bb died, wy sucked his teat in addition to her own although probably getting little if any milk from it after the first few days.

12's July litter

All but two members of this litter (pp and pw) died within the first ten days, but before this the upper row of teats were preferred to the lower row. By the third day, a stable teat order had formed with piglets on the anterior two right teats and the anterior six left teats. Piglets pp and pw preferred L6 and L5 respectively. However, by the end of the first week, pp had moved to teat L1.

An incidental observation was made of a piglet from WB's litter stealing an extra suckling from 12. When 12's piglets were eight days old, WB's piglet bo (who was a month older), sucked milk from 12's teat, L2, after dislodging its owner. WB had been suckling her litter in 12's farrowing nest at the same time as 12, and bo had jumped round to 12's udder immediately after suckling from his own teat.

The August litters

The suckling behaviour of RR's and 2's August litters was not observed until they were two weeks old, by which time stable suckling orders already existed, as shown in Table 1.7. When RR's piglet, yg died, yr obtained extra milk from her teat for a few days. Later, when piglets sometimes missed suckling bouts, their littermates sucked at their teats, particularly if they were more anterior to their own. For example, during a suckling bout observed when 2's piglets were twenty-five days old, five piglets were present at the udder, of whom so, bp and bs suckled from teats R4, L2 and L3, respectively, instead of from their own teats (L6, L5 and L4).

5 Suckling intervals

The interval between two successive sucklings with milk let-down ranged from 29 to 78 minutes over the first six weeks, and from 30 to over 200 minutes between six and ten weeks. (Observation sessions did not last for more than four hours, and so long suckling intervals are under-represented in the data.) Shorter intervals occurred between successive sucklings of which at least one was without milk let-down. These intervals ranged from 8 to 71 minutes over the first six weeks, and from 12 to 137 minutes, above six weeks. Table 1.8 shows the mean interval lengths and ranges for each litter and also gives the percentage of sucklings in which no milk let-down was recorded, which was in the range of 18 to 37 per cent. These results must be treated with caution, as they are taken from those sucklings which were observed closely enough to determine whether or not milk let-down had occurred. As the close

Table 1.8 Suckling intervals

Sow	Litter	Age period (weeks)	Mean interval length and range between two consecutive sucklings (minutes)				Unsuccessful sucklings	
			Both with milk let-down		One or neither with milk let-down			
			mean	range	mean	range	%	n
RR	February	0- 6	48.0	29- 75	25.3	12- 53	20.5	88
		6-10	65.8	41- 107	35.9	20- 62		
2	February	0- 6	59.8	56- 63	39.8	11- 71	36.8	68
		6-10	91.5	36- 154	39.3	12- 65		
12	February	0- 6	55.0	31- 78	31.8	12- 53	35.6	59
		6-10	62.3	30- 98	59.0	12-137		
WB	June	0- 6	51.4	37- 76	28.1	8- 58	22.2	54
RR	August	3-10	~100	70->200	~40	17->70	20.0	28
2	August	3-10	~100	40->200	43.8	30- 78	18.2	33

approach of the observer sometimes seemed to upset the sow, it is possible that sucklings occurring in the absence of the observer were more often successful. The results for the August litters were estimated, as the suckling intervals were longer than they had been in previous litters, and often only one successful suckling bout was observed closely per sow during an observation session.

For two litters, enough data was obtained to get a good estimation of the interval between two successful sucklings separated by one or more unsuccessful ones. For RR's February litter, between the ages of six and ten weeks, the mean interval was 74.4 minutes (range 49 to 107 minutes) and for WB's litter, between birth and six weeks, it was 58.5 minutes (range 42 to 93 minutes). The interval tended to be longer than that between two consecutive successful sucklings, but the ranges overlapped.

6 Initiation and termination of suckling bouts

Over the first few days of life, it was the sow which initiated suckling bouts, by grunting, approaching and sniffing her piglets (which roused them from sleep), and then lying on her side with her teats well exposed while grunting rhythmically. There was usually no obvious termination of a suckling bout at this young age, as the sow tended to remain on her side after milk let-down and the piglets continued to nose and suck the teats until they fell asleep in a huddle against the warm udder. Within two days, the piglets had learned to react to the grunts of the sow by approaching the udder and sucking their teats, even if the sow had apparently grunted in response to another pig passing by the nest, or for some other reason unrelated to a desire to initiate a suckling bout. However,

as the sow was willing to suckle her piglets frequently at this time, she would immediately respond to the approach of her piglets by grunting rhythmically and adopting a suckling position. Thus, it was often difficult to say whether it was the sow or the piglets who had initiated a suckling bout, as the responses of both were finely tuned.

As well as initiating suckling bouts by waking the piglets, disturbances at the nest site also terminated suckling bouts. For example, the attempted entrance of juveniles into the farrowing nest, or movements of the observer, provoked threats or chases from the sow, before or even during milk let-down. Sucklings were also sometimes terminated abruptly when piglets screamed during fights for teats or when they could not get to their teat due to crowding at the udder, and also when juveniles nosed at the udder and when adult and juvenile males were courting the sow.

Although over the first month the sows often led their piglets into a nest to suckle them, they increasingly suckled away from a nest site during periods of activity, especially when the weather was warm and dry. The first sucklings outside the nest occurred when piglets were between eight and thirteen days old. These sucklings were terminated within two minutes of milk let-down by the sow getting up and resuming her foraging behaviour, while the piglets moved off to forage, rest or play. If the suckling was unsuccessful, the piglets were likely to follow the sow, nosing at their teats and whining until she suckled them again. After the first few days of life, sucklings in the nest were usually terminated by the sow leaving the nest or rolling over onto her belly, preventing access to her teats.

As the piglets grew older, they required more food than the sow was able or willing to supply, and they took the main rôle in initiating sucklings, by approaching, whining, sucking and massaging their teats. Some members of a litter performed more of this behaviour than others, but it was not related to their weight relative to that of their littermates. The sow still determined the precise timing of sucklings, which occurred at various times after the arrival of piglets at the udder. She did not obviously wait until all piglets were present before suckling, with the result that piglets resting or active in other areas of the Pig Park tended to miss sucklings, or to come running up after let-down was over.

7 Synchronization of suckling bouts

Table 1.9 shows the number of sucklings with and without milk let-down which occurred within five minutes of a suckling by another sow. On average, slightly over one half of the observed sucklings were synchronized, which is significantly more than would be expected if sucklings occurred independently of one another at an average rate of once per hour ($\chi^2 = 21.17$; d.f. = 6; $p < 0.01$). Most of the observed cases of synchronization occurred when two sows were within ten metres of one another. If one sow started to suckle her piglets, other piglets in the vicinity usually went to their own mother and induced her to suckle also. It seems that the sows were responding to the suckling vocalizations of each other and their piglets as well as to stimulation of their udder by their piglets, as when WB suckled her litter, her mother, 4, often started grunting rhythmically as if she also was suckling. In fact, of sixteen sucklings by WB which occurred while 4 was nearby, 4 started grunting during nine of them,

Table 1.9 Synchronized suckling bouts

Sow	Litter	Number of times sow suckles within 5 minutes of another sow	Total number of suckling bouts	Per cent synchronized suckling bouts
RR	February	44	101	43.6
2	February	46	73	63.0
12	February	32	67	47.8
WB	June	7	16	43.8
12	July	11	14	78.6
RR	August	16	30	53.3
2	August	18	37	48.7

although the piglets did not nose her udder and she did not lie down on her side to present her udder. This response by 4 was most frequent when WB's piglets were between one and three weeks old, when 4 was resting regularly in WB's farrowing nest with WB and her litter.

Synchronized suckling was most common between sows which regularly rested together. In the Spring, sows RR and 2 were more likely to suckle with each other than with 12, while in the Autumn, WB and 12 suckled together, as did RR and 2, but they only occasionally suckled with a member of the other pair of sows.

8 Weaning

Table 1.10 gives the age of each litter when (a) the sow first behaved aggressively towards piglets, (b) when one or more piglets first missed a suckling bout and (c) when weaning from milk was completed. An exact age at weaning could not be given as the suckling intervals became very long towards the end of weaning. Also, it is not known when WB and 12 first acted aggressively towards their piglets, as they were not under observation during their second

Table 1.10 Weaning behaviour

Sow	Litter	Age (days) Sow first aggressive to piglets	Litter members first miss a suckling	Weaning completed
RR	February	46	25	96-98
2	February	40	29	92-94
12	February	53	32	80-88
WB	June	94	36	97-100
12	July	70	no absences observed	80-83
RR	August	47	26	63-73
2	August	17	17	60-64

month of lactation. However, WB was notably unaggressive during weaning, and tended to walk or scamper away from her piglets when they demanded milk, rather than swinging round and snapping at them. She also remained relatively willing to suckle them for longer than the other sows, and her piglets seemed to wean themselves as she sometimes suckled only one or two while the other(s) stood by and made no attempt to suckle. On one occasion, when her ninety day old piglets were in another part of the Pig Park, WB lay down on her left side grunting (as 12 suckled her piglets), and some of 2's seventeen day old piglets nosed and sucked at her teats. Others approached 2 and were snapped at. Piglets ss and so, who were sucking at WB's enlarged teats R1 and R4, received a milk let-down from WB, while bb and bs sucked at the small dry teats, R2, and R5. (These were not their regular teat positions.)

Sow 12 also seemed fairly unaggressive towards her July piglets, and continued to suckle them both until they were at least eighty days old. However, when they were eighty-three days old, pw was observed to sniff 12's nose and then jump aside giving a low grunt, which would suggest that he expected to receive aggression

from her.

Although sows RR, 2 and 12 started to show aggression towards their February litters when they were forty to fifty-three days old, they continued to suckle them until they were at least eighty days old. RR was the least aggressive of the three, and suckled for the longest period. Sow 2 was the most aggressive, continually snapping at and walking away from her piglets, but they persisted in following her and whining until she suckled them. Towards the end of and after weaning, they were wary of her and backed away rapidly when she moved her head, even when she showed no signs of aggression.

Some of 12's piglets were frequently absent from sucklings and seemed to wean themselves (pw, pbl, pg and wbl) while others persisted in their attempts to suckle and were snapped at by 12 (pb, pr, wo and wg). In order to determine whether differences in suckling behaviour, between six weeks of age and weaning, were correlated with differences in other behavioural traits, the behavioural frequencies of the members of these two groups of piglets were compared. Both groups were of approximately the same weight (119.5 kg versus 123.1 kg at eighty-one days of age). The persistent sucklers performed significantly more rapid grunting, squealing, sucking and massaging, switching rapidly between teats and playing than the abstaining group, which spent more time standing and lying in contact.

The two August litters were both weaned three to four weeks earlier than the previous litters, despite similar growth rates. They were suckled less frequently and missed fewer sucklings, and their mothers apparently played the main rôle in weaning them,

although RR was less aggressive than 2.

III Resting behaviour

1 Effect of age

Figure 1.5 plots changes in the number of thirty second intervals spent lying down and standing up as the piglets grew older. (See Appendix B.2 for a detailed list of frequencies.) In their first eight days, they were more likely to stand in contact with one another than apart, but after this, they usually stood out of contact as they were more active. Also, the time spent lying resting in contact during daytime observation sessions declined from its initially high level. The most common position used while resting was lying on the belly, but lying stretched out on the side, sitting and kneeling also occurred during resting bouts. Occasionally, the piglets rested out of contact with others, particularly on warm, dry days when they lay down for short rests in between foraging bouts.

2 Effect of time of day

More time was spent lying resting in contact between 1500 hours and 0900 hours than during the daytime at all ages. During the night, the piglets were observed to leave the nest after suckling bouts in order to urinate but they soon returned to rest. Adults and juveniles resting with them sometimes left at the beginning of a suckling bout, to eliminate and to forage nearby, having been aroused by the upheaval in the nest created by whining piglets crawling over them and the movement of their mothers into suckling positions.

After the age of eighteen days, the piglets were most active between 1100 hours and 1300 hours, spending the least time resting

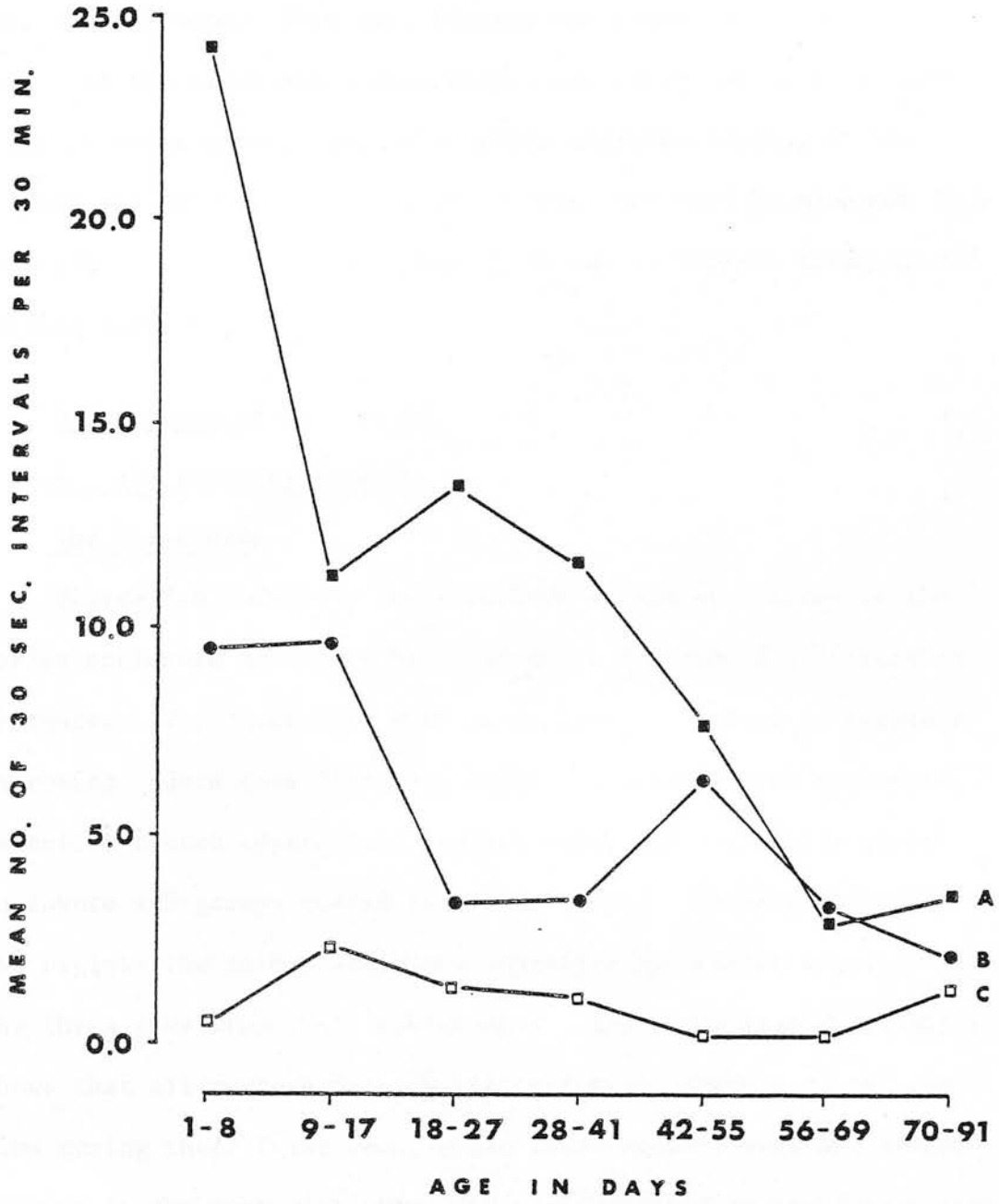

Figure 1.5 Changes in the number of intervals in which (A) lie, sit, kneel in contact, (B) stand in contact and (C) lie, sit, kneel apart occurred with age

and the most time rooting and playing compared with other times of day, whereas before this age, resting was common at all times of day. At the older ages, the piglets generally followed the movements of their mothers and other group members, feeding at the feeding site between 1000 and 1100 hours, followed by movement to a drinking site for water and then by movements between foraging and resting sites.

3 Resting relationships

A The February litters

The first week

Figure 1.6 indicates the locations of the nest sites in the forest enclosure after the birth of RR's, 2's and 12's litters in February. The three sows with their litters rested in separate farrowing nests (see Plate 3), while the seven forest enclosure juveniles rested together in another nest, and the entire gorse enclosure sub-group rested in a fifth nest. (Before the birth of the piglets the forest enclosure juveniles had rested together with the three sows from their sub-group.) The dendrogram in Figure 1.7 shows that all members of each litter rested together at the same time during their first week, while their mothers were not always present in the nest with them, and are connected on the dendrogram at a lower level of similarity. The piglets tended to remain in and around the nest site while their mothers left to feed, drink and eliminate.

Maternal aggression was important in preventing other animals from resting with the piglets during this period. A stare or rapid movement of the sow's head towards an intruder was usually

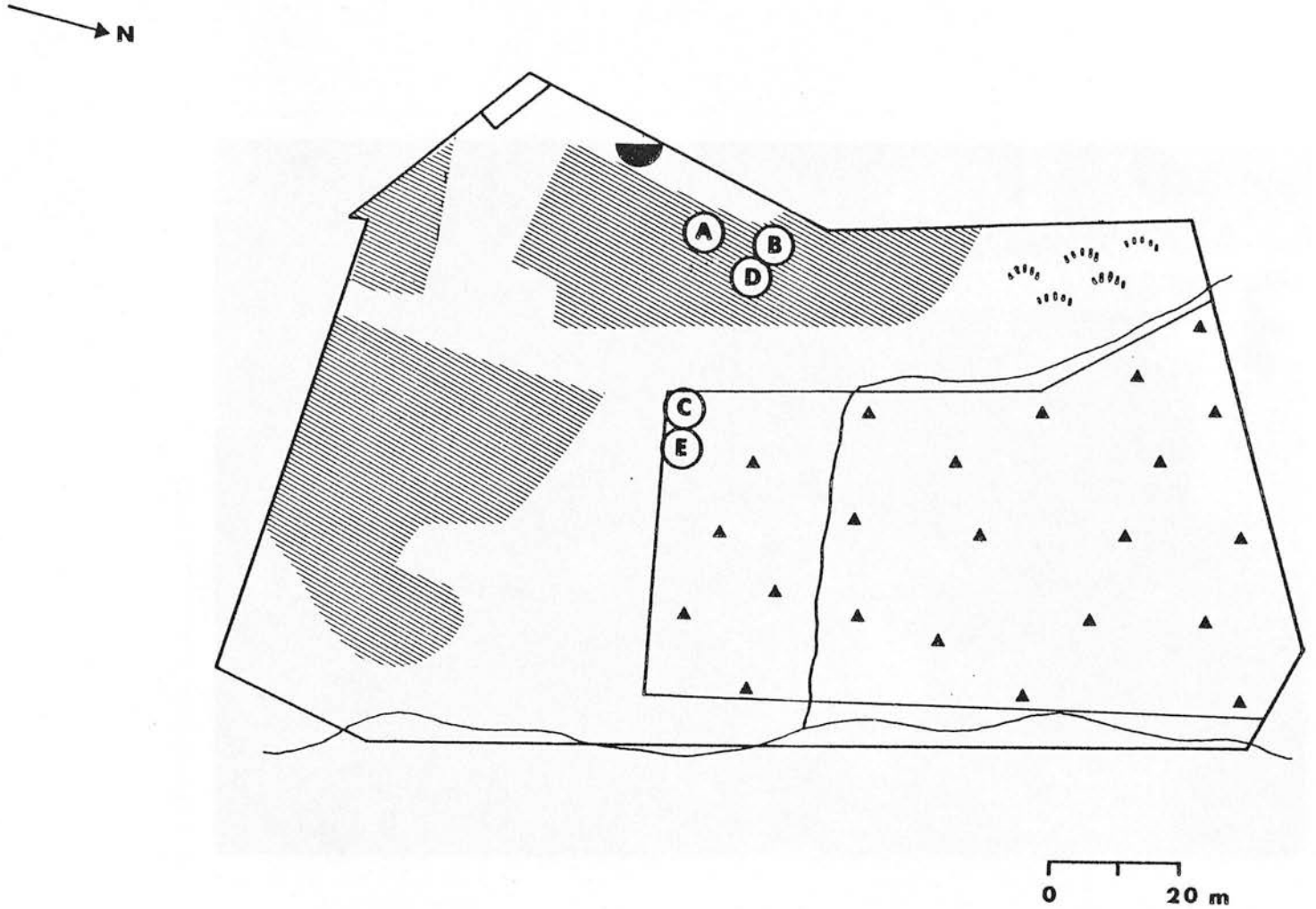

Figure 1.6 Nest sites used by the pigs in the forest enclosure between February and May, 1980 (A - RR's farrowing nest, B - 2's farrowing nest, C - 12's farrowing nest, D - Forest enclosure juveniles' nest, E - Gorse enclosure group's nest)

Plate 3 Sow 2 lies ready to defend her farrowing nest and her four day old piglets, which are active in the area around the nest

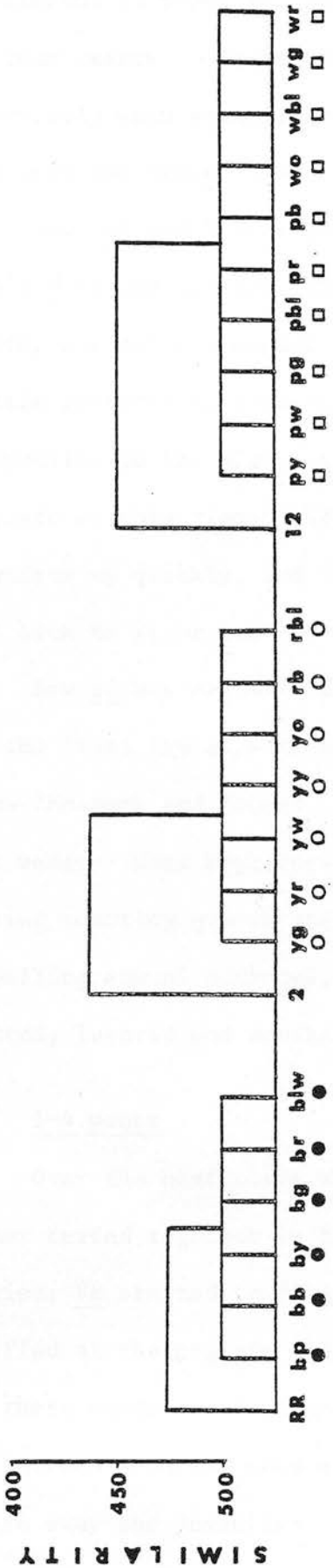

Figure 1.7 Dendrogram of the resting associations of the February litters; 0-1 week

● RR's piglets, ○ 2's piglets, □ 12's piglets

sufficient to repel it, but if not, it was bitten and chased for up to four metres. Aggression was also directed at the observer, especially when attempts were made to remove the young piglets from the nest for weighing and ear-tagging.

Sows RR and 2 were highly aggressive towards the juveniles from their previous litters, who frequently attempted to enter their nests, whereas the members of the gorse enclosure sub-group showed little interest in resting with them. The two sows were also very responsive to the high-pitched screams and squeals of all young piglets at this time. If lying in their nest, they would react by standing up quickly, and if away from the nest, they would either run back to it or run to the source of the disturbance.

Sow 12 was sexually attractive to the boar and male juveniles on the first few days after farrowing (although not fertile at this time (Holness and Hunter, 1975)), and frequently chased them out of her nest. They kept returning to sniff her anogenital region while giving courting grunts and champing their jaws. However, although repelling sexual advances, she gave no reaction when juveniles butted, levered and mouthed roughly at her young piglets.

1-4 weeks

Over the next three weeks, piglets from different litters sometimes rested together in the same nest. At the beginning of this period, RR started leading her piglets into 2's nest, where they sniffed at the piglets and then returned to rest in their own nest. On these occasions no aggression was observed between the two sows or between them and each other's piglets, although they continued to chase away the juveniles. RR and her piglets first remained and

rested in 2's nest when the piglets were twelve days old, and on the same day juveniles were tolerated by the sows when they entered the nest. Some juveniles also rested in RR's vacated nest after being driven from their own nest by WB. Over the next few days RR, 2 and their piglets frequently rested together in 2's nest, while the forest enclosure juveniles mainly used RR's nest and the gorse enclosure sub-group used the juveniles' former nest (see Figure 1.6). Juveniles also rested occasionally in 12's nest at this time. When 12's piglets were fifteen days old, she started resting with her piglets and the juveniles in RR's nest. During the fourth week, RR and her litter often rested in this nest along with 12 and her litter, while 2 and her litter used her own and also 12's nest. The juveniles rested with the various sow and piglet groups, but the gorse enclosure sub-group rested separately on all but one occasion, when the boar (7) rested with 12 and her litter.

The dendrogram in Figure 1.8 illustrates the resting associations during this period. As littermates continued to rest together most frequently, along with their mother, three distinct clusters are formed on the dendrogram at a similarity of 377. However, the members of each litter are no longer all connected at the same similarity level as they did not always rest together at the same time. Further up the dendrogram, it can be seen that RR's and 2's litters are connected at a similarity of 309. This represents the similarity between 2's piglet blw and RR's piglet bp. As described in the section on suckling behaviour, blw was initially a member of RR's litter, but he switched to 2's litter when he started suckling from 2. During the first few days of this period he rested with RR's litter, but after this he rested mainly with 2's

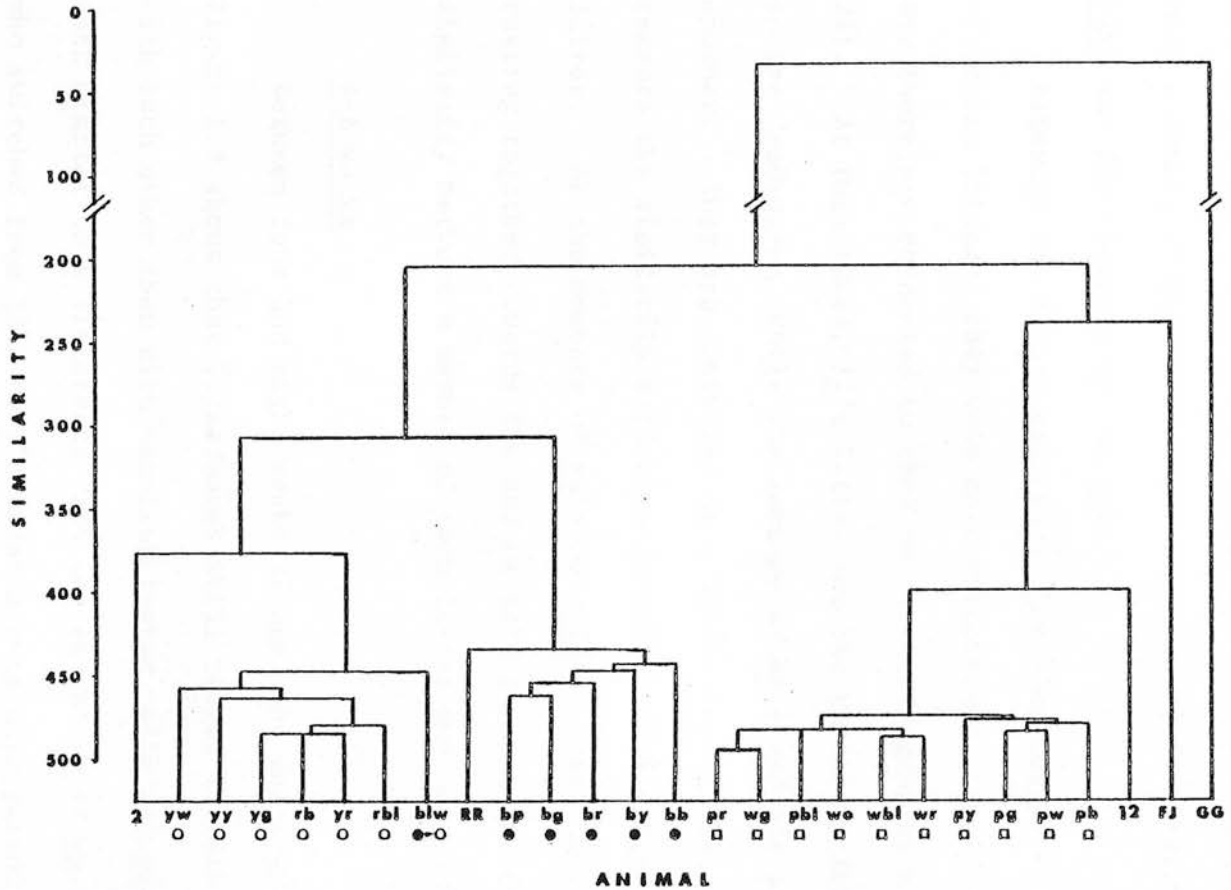

Figure 1.8 Dendrogram of the resting associations of the February litters; 1-4 weeks (FJ - Forest enclosure juveniles, GG - Gorse enclosure group)

○ 2's piglets, ● RR's piglets, □ 12's piglets

(Piglet blw switched litters)

litter, and therefore, his highest similarity (449) was with a member of 2's litter. However, his similarity of 309 with bp was the highest similarity between a member of 2's litter and a member of RR's litter, thus connecting the two clusters on the dendrogram at this level. Nevertheless, other members of the two litters also rested together during this period, and the highest similarity between a member of RR's litter and a member of 2's litter, other than blw, was 286 (between bp and rbl).

Although the forest enclosure juveniles rested with members of all three litters, they were most often found with 12's piglets and are therefore connected to them on the dendrogram at a similarity of 241. At this level, 12's litter and the juveniles form one cluster on the dendrogram, while the members of RR's and 2's litters form another. They are connected at a similarity of 205, which represents the similarity between a juvenile and a member of RR's litter. As the members of RR's and 12's litters only started resting together towards the end of this period, the highest similarity between a member of each litter was only 138.

4-8 weeks

Between four and eight weeks of age, the dendrogram in Figure 1.9 shows that littermates still tended to rest more often with each other than with non-littermates, with all piglets being most similar to a littermate with the exception of wg. Piglet py, who switched from 12's to 2's udder during this period, was now resting mainly with her new littermates. Members of RR's and 12's litters often rested together in RR's nest, and are connected to 2's litter on the dendrogram by the similarity between py and bp. At this similarity level (333), B_2 cluster analysis (see Methods)

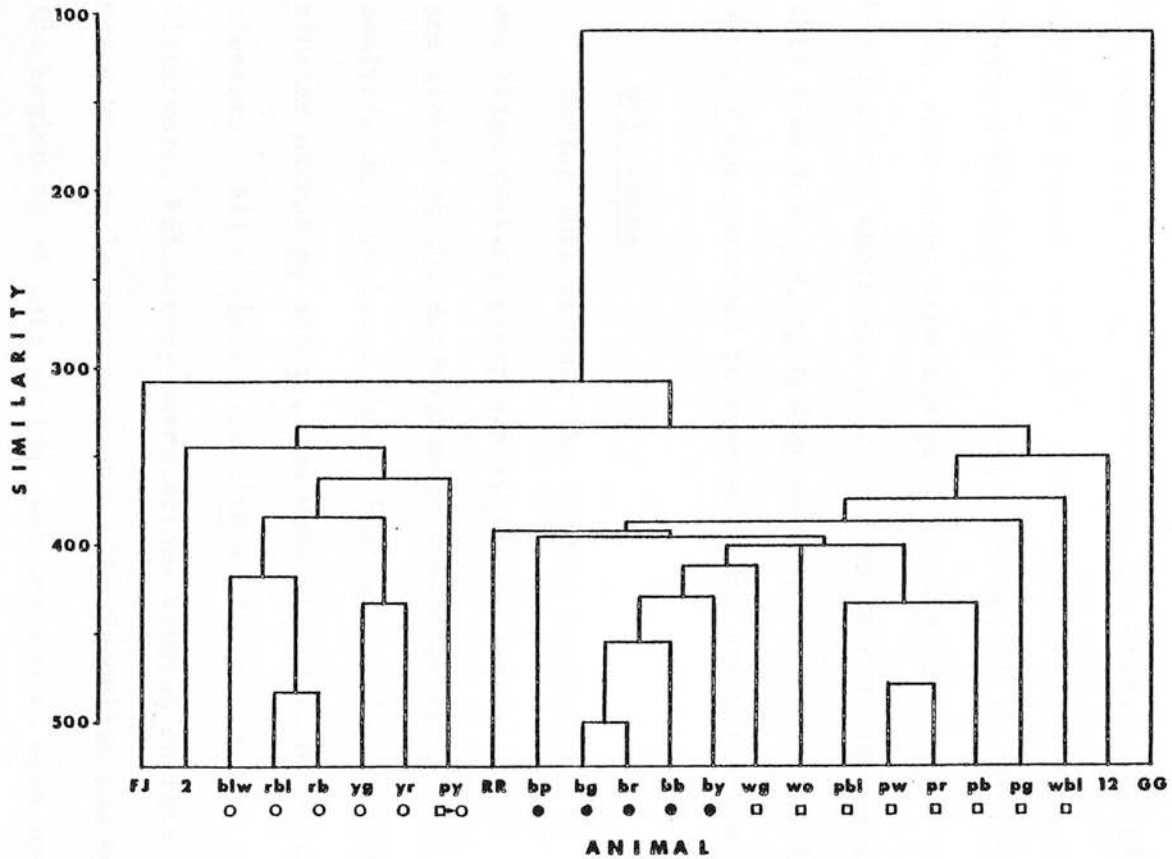

Figure 1.9 Dendrogram of the resting associations of the February litters; 4-8 weeks
(FJ - Forest enclosure juveniles, GG - Gorse enclosure group)

○ 2's piglets, ● RR's piglets, □ 12's piglets
(Piglet py switched litters)

showed that 2 and her piglets formed one cluster, while 12, RR and their piglets belonged to another. Certain pairs of piglets appeared to have relatively strong resting associations during this period, these being rbl and rb, bg and br, br and bb, and pw and pr, all of which were connected at similarities greater than 450.

The gorse enclosure sub-group rarely rested with the piglets, but regularly used 2's nest while 2's litter used 12's nest and RR's and 12's piglets used RR's nest. On one occasion, 4 and R were observed resting in RR's nest with all of the piglets and at another time, when rain, snow and gale-force winds flooded all of the nests but 2's, the whole pig group rested in that one nest. (It was at this time that yw, yy and wr were crushed.) Finally, when 2 was on heat, 7 was observed to rest with her and her litter.

8-13 weeks

During this period, the further integration of the piglets into one large resting group was apparent (Figure 1.10). All piglets are linked on the dendrogram at a similarity of 250, and B_2 cluster analysis at this level showed that all piglets belonged to the same cluster except py and rb, who were linked to only one member of the cluster. All piglets except rb still rested most often with a littermate, but strong associations between certain pairs of littermates were no longer apparent. The juveniles had been removed at the beginning of this period, and the adults were now relatively peripheral to the piglet group.

B The June and July litters

The first week

When the gilt WB gave birth to her first litter in June, she

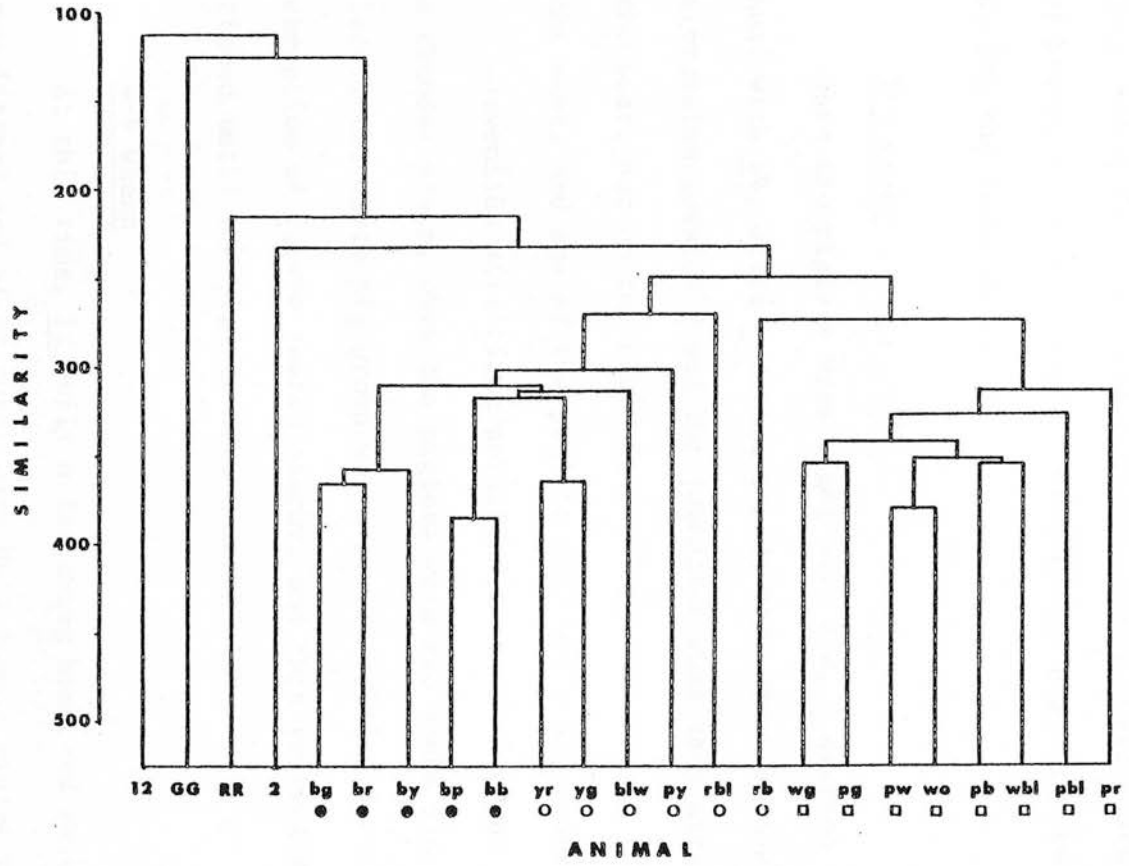

Figure 1.10 Dendrogram of the resting associations of the February litters; 8-13 weeks
(GG - Gorse enclosure adults)

● RR's piglets, O 2's piglets, □ 12's piglets

did not defend her farrowing nest but allowed her mother, 4, and the boar, 7, to enter it and lie down, crushing seven of her piglets. Human intervention persuaded 4 and 7 to leave but WB showed little aggressiveness over the first two days. However, on subsequent days, she threatened the juveniles from the February litters when they looked into her nest with the result that, apart from the day of birth, no other animals rested in her nest with her piglets during the first week.

1-4 weeks

When the piglets were eight days old, 4 started resting in the nest with WB, while 7 rested beside it. Both sows showed aggression towards 7 and the juveniles when they attempted to enter the nest, but on the eleventh morning, 7 was found resting inside the nest, and one of the piglets (bb) had been crushed.

Juveniles were first permitted to rest with the piglets, during a thunder storm, when the piglets were two weeks old. A week later, the whole pig group was observed resting in the nest with the exception of 7, who rested nearby, and this resting arrangement continued until the piglets were a month old.

4-6 weeks

At this time, 12 built a farrowing nest and gave birth to her new litter, and after three days WB's female piglet wy entered 12's nest to rest. That night, wy and her brothers, bp and bo rested in 12's nest, and 12 showed no aggression towards them although they snapped at her piglets. However, WB did not enter the nest but rested beside it. On subsequent occasions, WB rested in the nest with 12 and the piglets, and a number of 12's piglets were crushed.

Both sows were relatively unresponsive to the distress vocalizations of young piglets (compared with 2 and RR, while they were lactating). For example, when WB was observed lying on top of one, which was screaming, neither sow moved.

Figure 1.11 shows the locations of the nests used by the pigs during this set of observations, while Figure 1.12 shows a series of dendrograms illustrating their resting relationships, as described above.

C The August litters

0-4 weeks

Sows 2 and RR farrowed in widely separated nests (Figure 1.13) and no other pigs were found resting in them until the piglets were twelve and fifteen days old, respectively, when RR led her litter into 2's nest to rest. After this, they regularly rested together, while the remainder of the group immediately started to use RR's vacated nest, which was more sheltered.

The juveniles (from WB's and 12's litters) were first observed resting in 2's nest with piglets when the piglets were twenty-three and twenty-six days old. They snapped at the piglets, causing them to squeal and run aside, but when 2 later returned to the nest, she chased them away.

On the dendrogram for the period between one and four weeks (Figure 1.14), the piglets are separated into their respective litters at a similarity of 477, and B_2 cluster analysis produced two clusters, containing all members of each litter. As the piglets started resting together during this period, they are linked on the dendrogram at a similarity of 372, and as the juveniles only

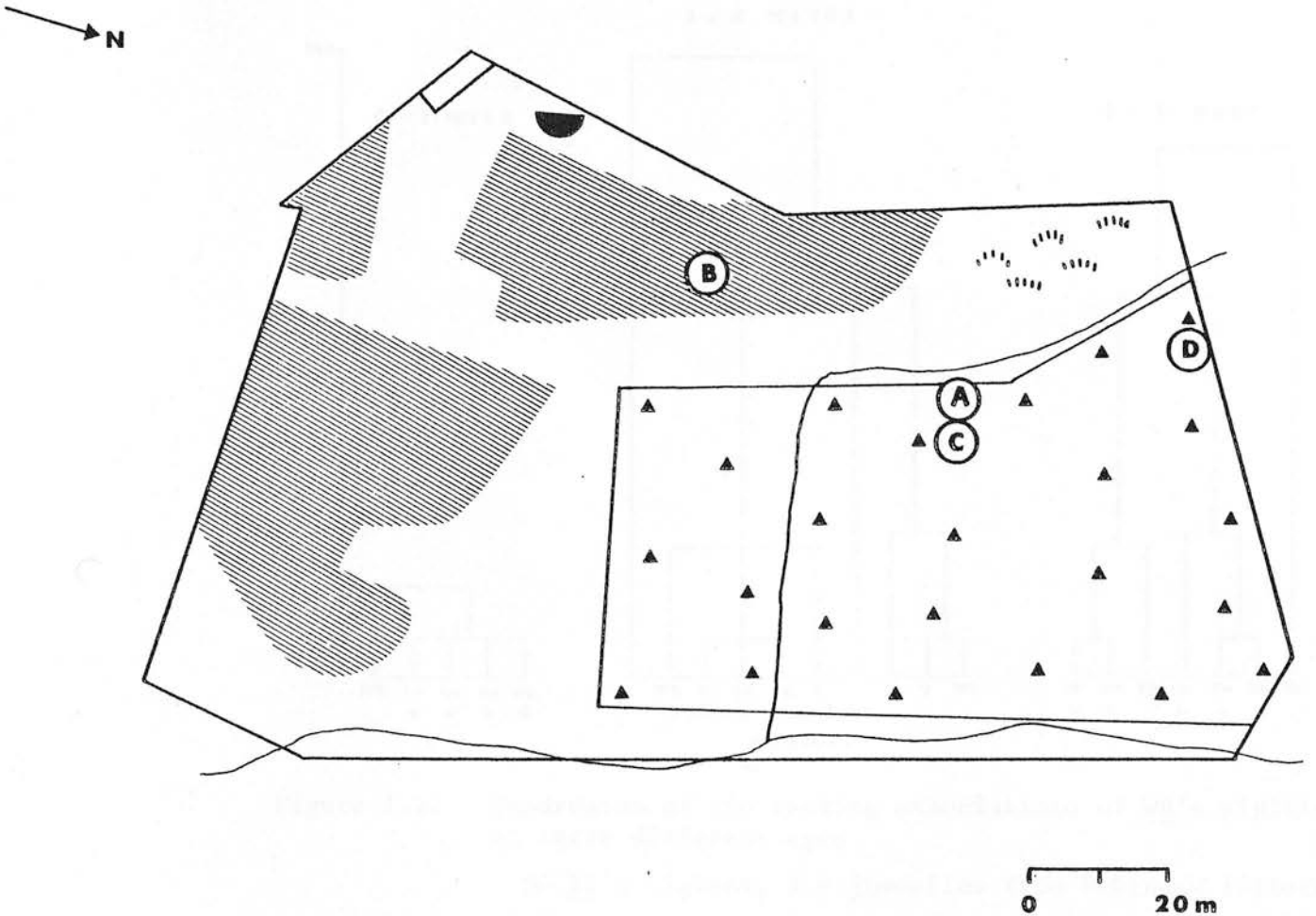

Figure 1.11 Nest sites used by the pigs in the forest enclosure in June and July, 1980 (A - WB's farrowing nest, B - 12's farrowing nest, (C) - Juveniles' nest, D - Adults' nest)

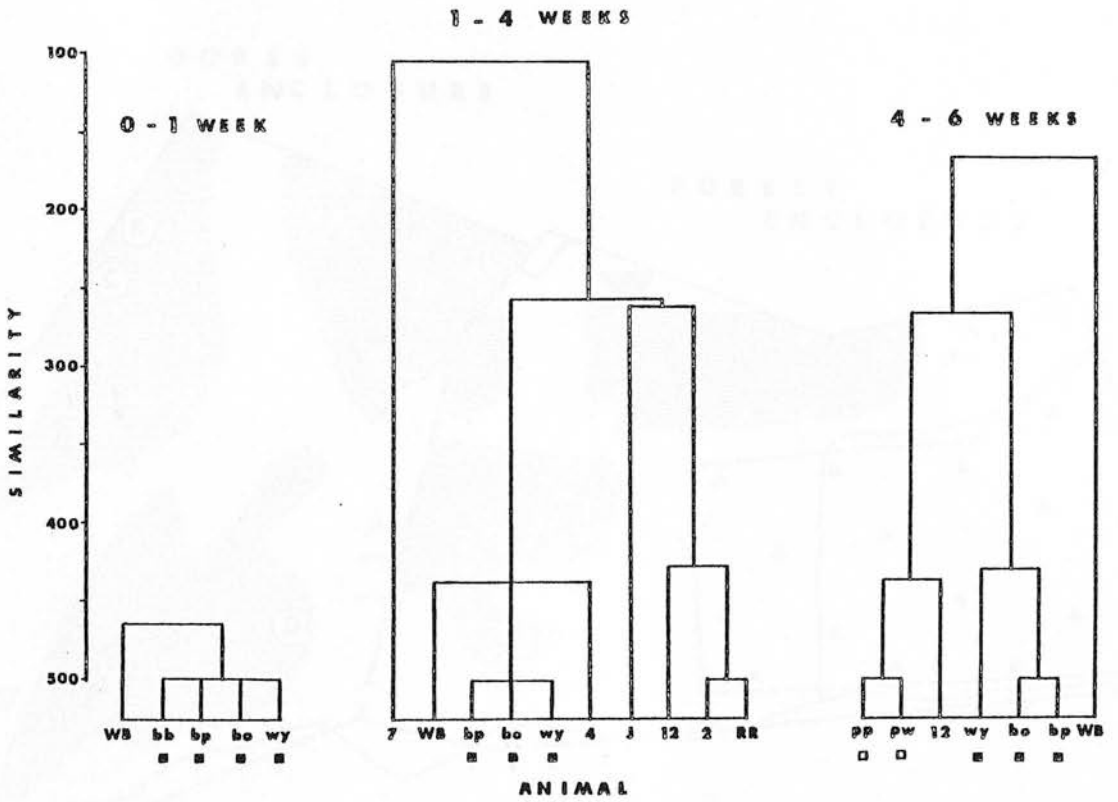

Figure 1.12 Dendrogram of the resting associations of WB's piglets (■) at three different ages

□ 12's piglets, J - juveniles from February litters

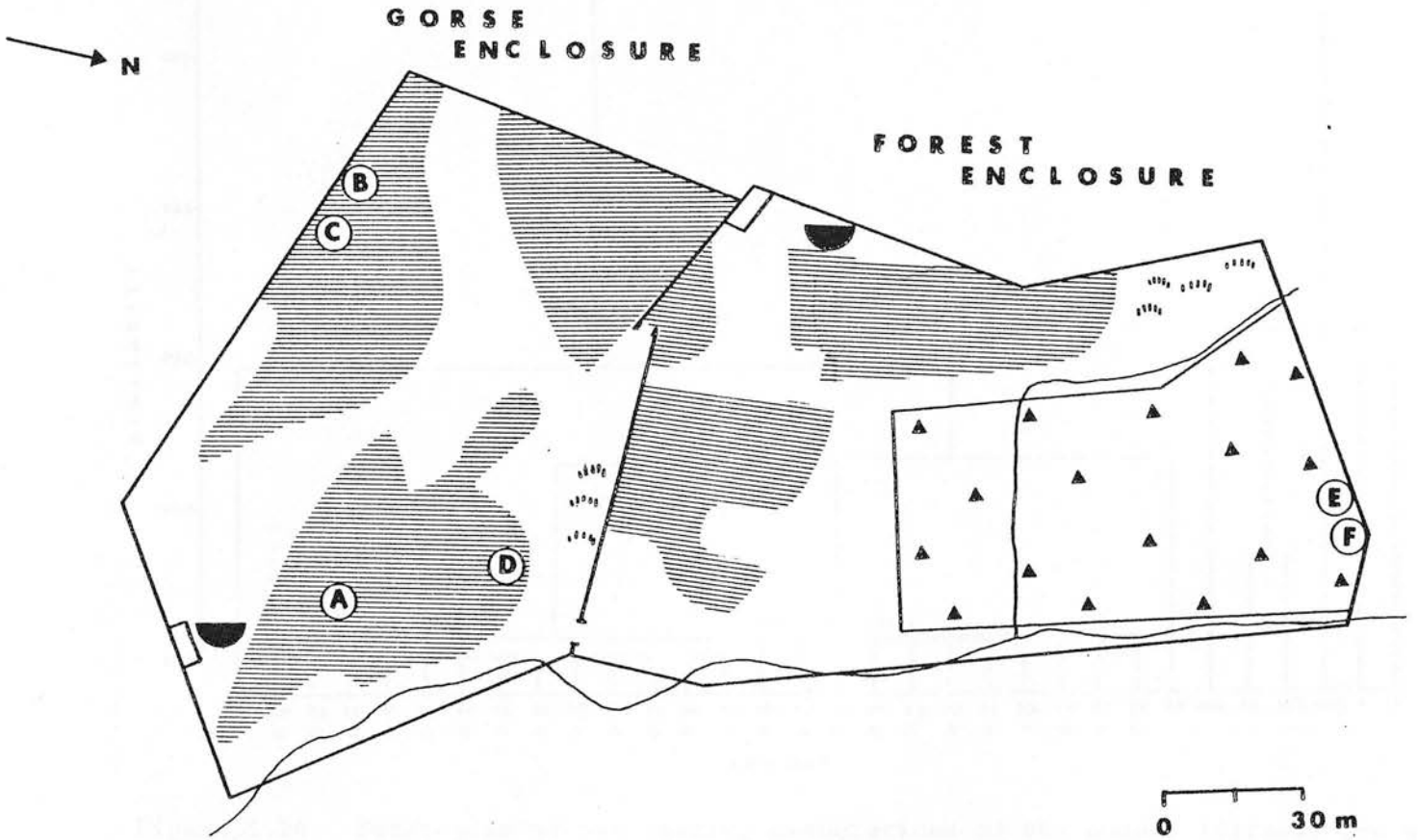

Figure 1.13 Nest sites used by the pigs in the Pig Park between August and November, 1980 (A - 2's farrowing nest, B - RR's farrowing nest, C - Adults' and juveniles' nest, D, E and F - new nests)

gorse, feeding site, bog, woods, stream

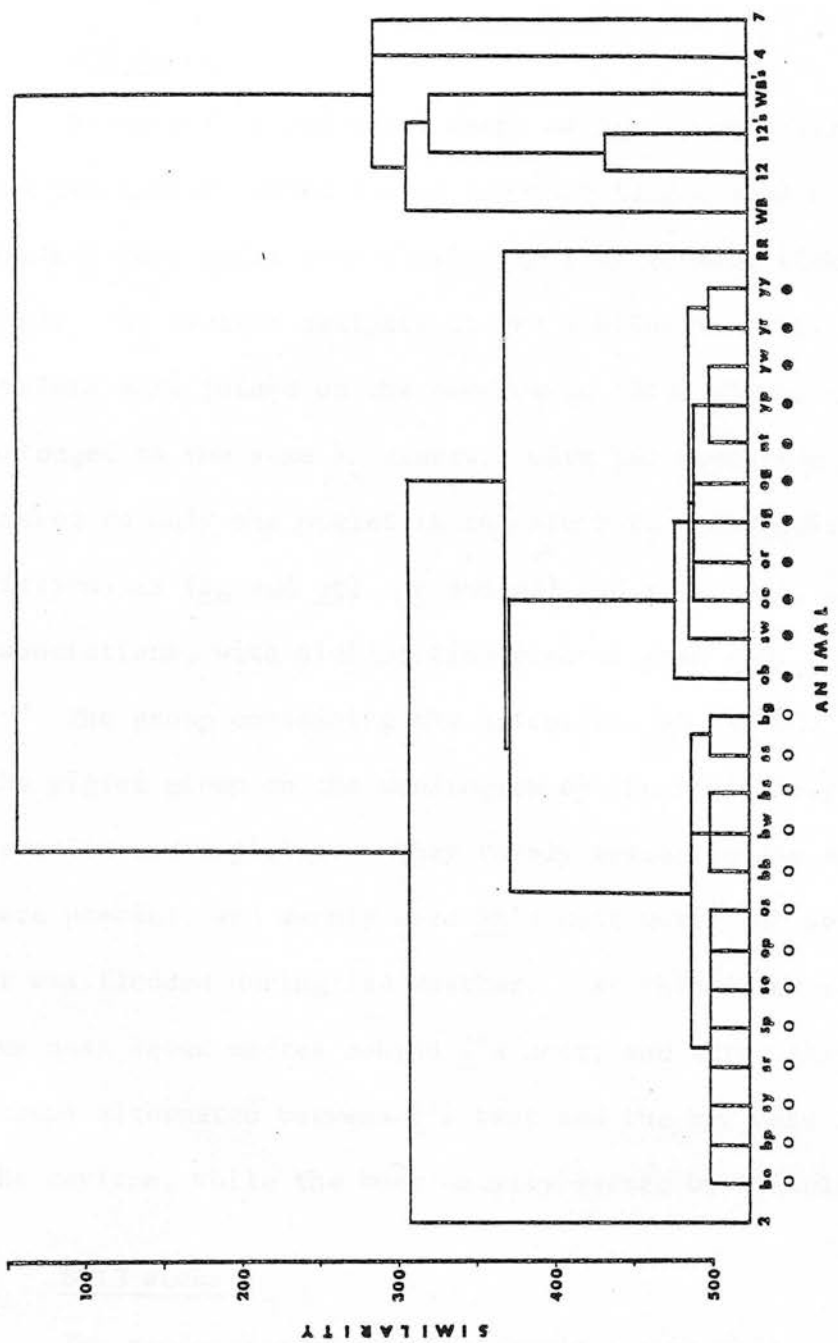

Figure 1.14 Dendrogram of the resting associations of the August litters; 1-4 weeks

○ 2's piglets, ● RR's piglets (12's and WB's - piglets of 12 and WB)

occasionally rested with the piglets, the group containing them, their mothers, 4 and 7, is connected at the low level of 56. RR and 2 spent relatively less time resting with their present litters than they had with their Spring litters.

4-8 weeks

Between four and eight weeks of age (Figure 1.15), members of the two litters often rested together in 2's nest although all piglets were still most similar to a littermate with one exception (sp). B_2 cluster analysis at the similarity level at which all piglets were joined on the dendrogram (353) showed that they all belonged to the same B_2 cluster, with the exception of ob, who was linked to only one piglet in the cluster. Two pairs of male littermates (sg and or; or and sw) had relatively strong resting associations, with similarities greater than 450.

The group containing the juveniles, WB, 12 and 4 was linked to the piglet group on the dendrogram by the similarity between a juvenile and a piglet. They rarely rested in 2's nest if RR or 2 were present, and mainly used RR's nest until the seventh week, when it was flooded during bad weather. At this time, they moved to a new nest seven metres behind 2's nest, and after this, the two groups alternated between 2's nest and the new nest for rests during the daytime, while the boar usually rested by himself.

8-13 weeks

The dendrogram of resting groups during this period (Figure 1.16) shows that all piglets were linked together at a similarity of 327. They all belonged to one B_2 cluster at this level, except for ob and ss, who were each linked to only one member of the cluster. Of the

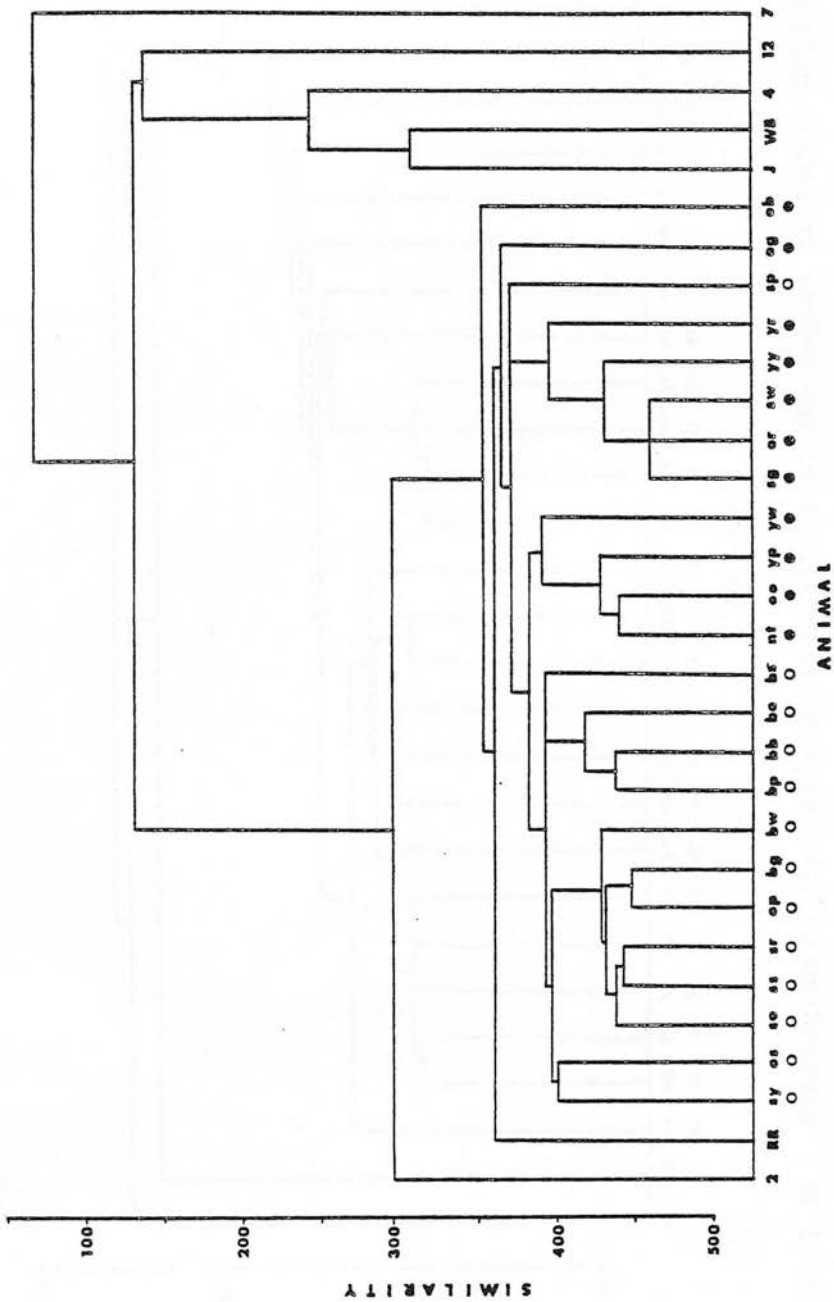

Figure 1.15 Dendrogram of the resting associations of the August litters; 4-8 weeks
○ 2's piglets, ● RR's piglets, J - juveniles from February litters

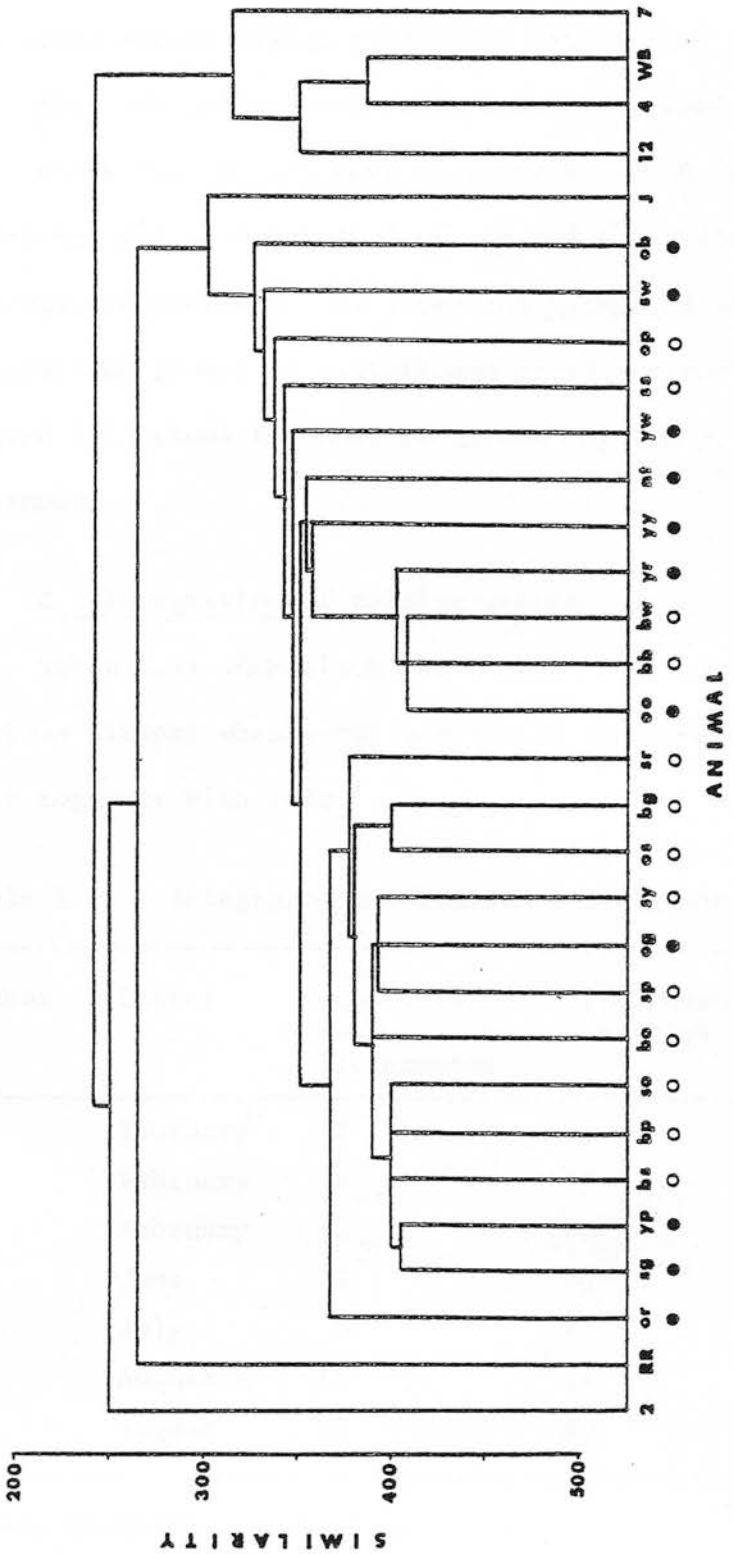

Figure 1.16 Dendrogram of the resting associations of the August litters; 8-13 weeks

● RR's piglets, ○ 2's piglets, J - juveniles from February litters

twenty-four piglets, eighteen were most likely to rest with a littermate, while six rested more often with a non-littermate. The juveniles frequently rested with the piglets while their mothers and the other adults rested relatively little with them.

When the animals were shut into the forest enclosure in the eleventh week, two new nest sites were chosen in the woods. The upper one was used mainly by 2, RR and the piglets, while the lower one was frequented by the juveniles 4, WB, 12 and 7, although during the daytime groups of piglets and juveniles rested in both nests. Figure 1.13 shows the nest sites used by the pigs between August and November.

D Integration of resting groups

Table 1.11 summarizes the results by showing the ages of the various litters when other members of the group first started to rest together with them.

Table 1.11 Integration of litters into larger resting groups

Mother	Litter	Age of litter (days) when first rest with: Non-littermates	Juveniles	Adults (other than dam)
RR	February	12	12	12
2	February	8	8	8
12	February	12	12	24
WB	June	31[a]	14	0
12	July	3	65[b]	4
RR	August	15	26	15
2	August	12	23	12

[a] none available until 28 days old

[b] none available between one and six weeks of age

IV Social facilitation

1 Changes with age

The behaviour patterns considered here are those performed during periods of activity which, although not directed at other animals, can nevertheless be socially facilitated. From Figure 1.17, it can be seen that the proportion of time spent walking and sniffing at the ground increased with age. During the first six weeks, rooting into the earth was often performed in a perfunctory manner and often appeared playful. It dropped in frequency at the beginning of weaning but later rose in frequency in the context of digging for and eating roots. Similarly, whereas sniffing and biting at objects was initially done during investigation of solid objects, including inedible ones (e.g. stones, bits of metal), it was later performed mainly during foraging on tree roots and branches.

Figure 1.18 shows that shovelling, which was performed by young piglets in the context of arranging and burrowing into the straw before lying down, rose to a peak between the fourth and sixth week, when it was often performed playfully by groups of piglets as they entered a nest. Its frequency dropped during weaning but then increased, especially during foraging, when it was done to remove loose earth from a rooting hole. Levering up and tugging at branches and roots also increased as foraging for food became more important, but carrying objects in the mouth and shaking them remained rare. Adults carried branches to the nest site during nest building, and, on rare occasions, shook animals such as rabbits to kill them, but piglets were never observed to do such things. The frequency of nosing and chewing at the observer's clothing was

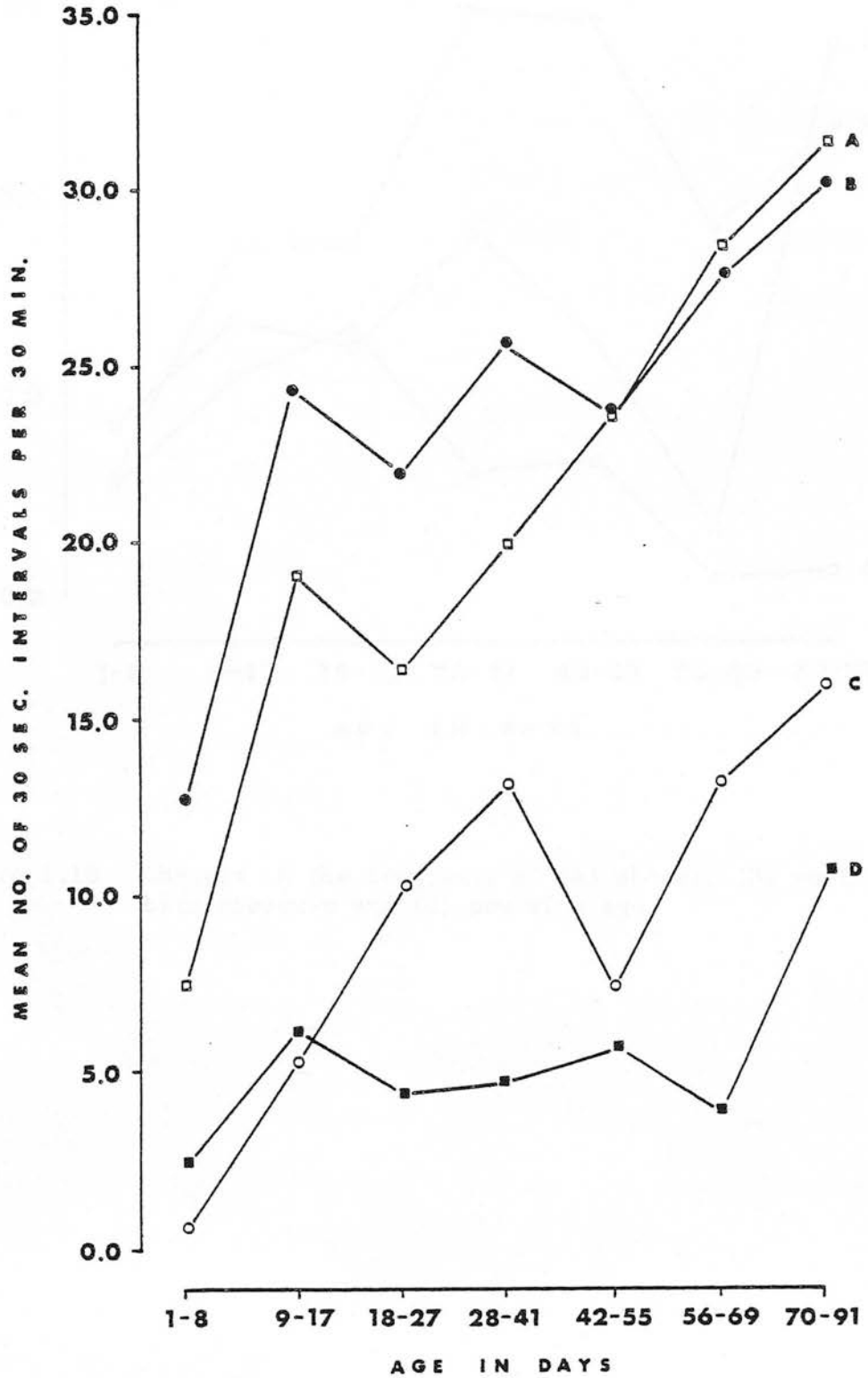

Figure 1.17 Changes in the number of intervals in which (A) sniff ground, (B) walk, (C) root, and (D) sniff/bite objects occurred with age

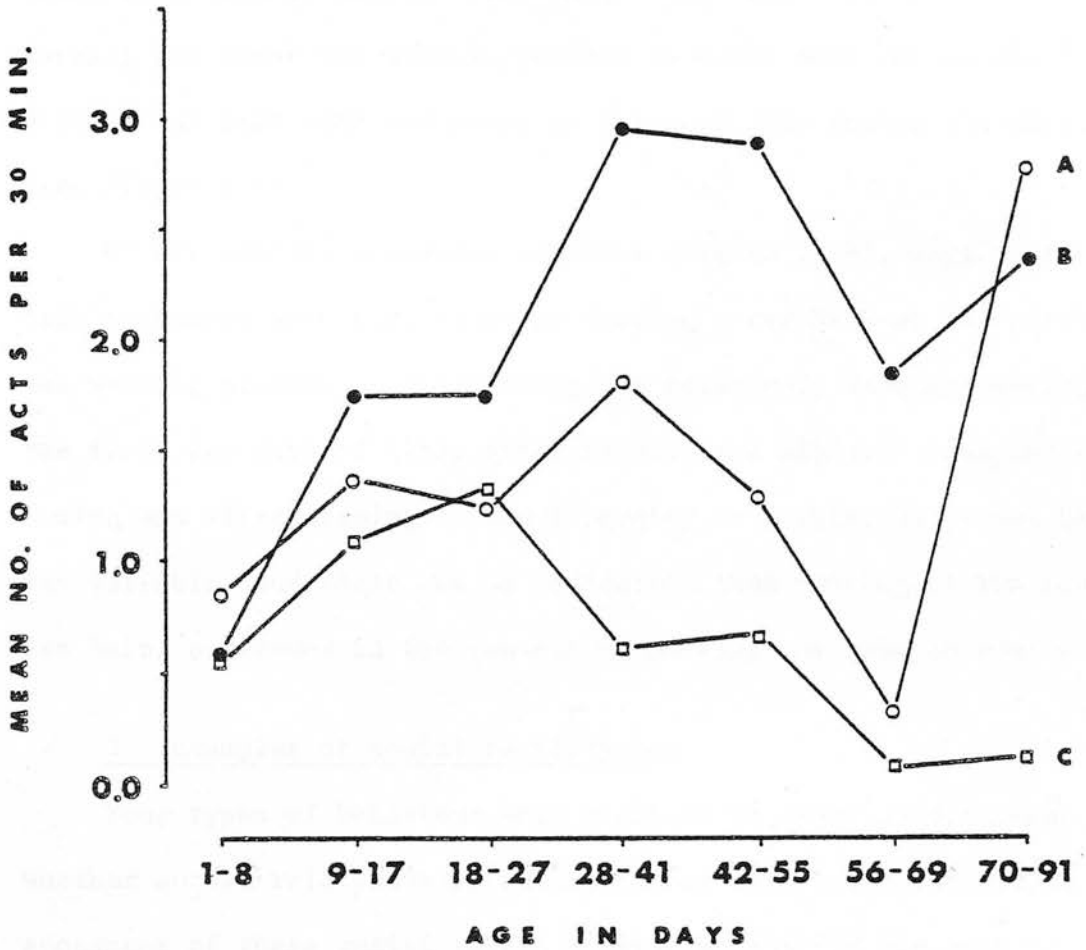

Figure 1.18 Changes in the frequency of (A) shovel, (B) sniff, bite observer and (C) paw with age

highest during the fourth to sixth week, while pawing, which was associated with arranging straw in the nest and with elimination (during the first two weeks), reached an early peak and declined with age as less time was spent at the nest site during the daytime (see Figure 1.18).

Of the comfort behaviour patterns (Figure 1.19), wagging the tail increased with age, although showing a set-back at the start of the weaning process. Headshaking was relatively frequent during the first few days of life, after tagging the piglets' ears, and also during and after weaning. The frequency of rubbing and scratching was variable, and there was no indication that rubbing of the head was being performed in the context of marking, as seen in adults.

2 Examples of social facilitation

Four types of behaviour were analysed in order to determine whether social relationships were apparent from inter-individual sequences of these activities. To give an idea of the sort of sequences under consideration, an example is given for each behaviour. Appendix F gives information on the number of inter-individual bouts of each activity recorded at different ages.

Rubbing and scratching

This example comes from the February-born piglets when they were nine weeks old. Sow 12 started to rub her head and side against a tree (and continued to do so throughout the bout). Piglet bp then squatted and rubbed her behind on the ground and stepped forward to rub her side up and down against a tree. Piglet pr then rubbed her side, followed by bb, who rubbed her behind against a log while pb rubbed her side. Piglet bp then scratched her thigh with her other foot, and bg scratched her neck with her

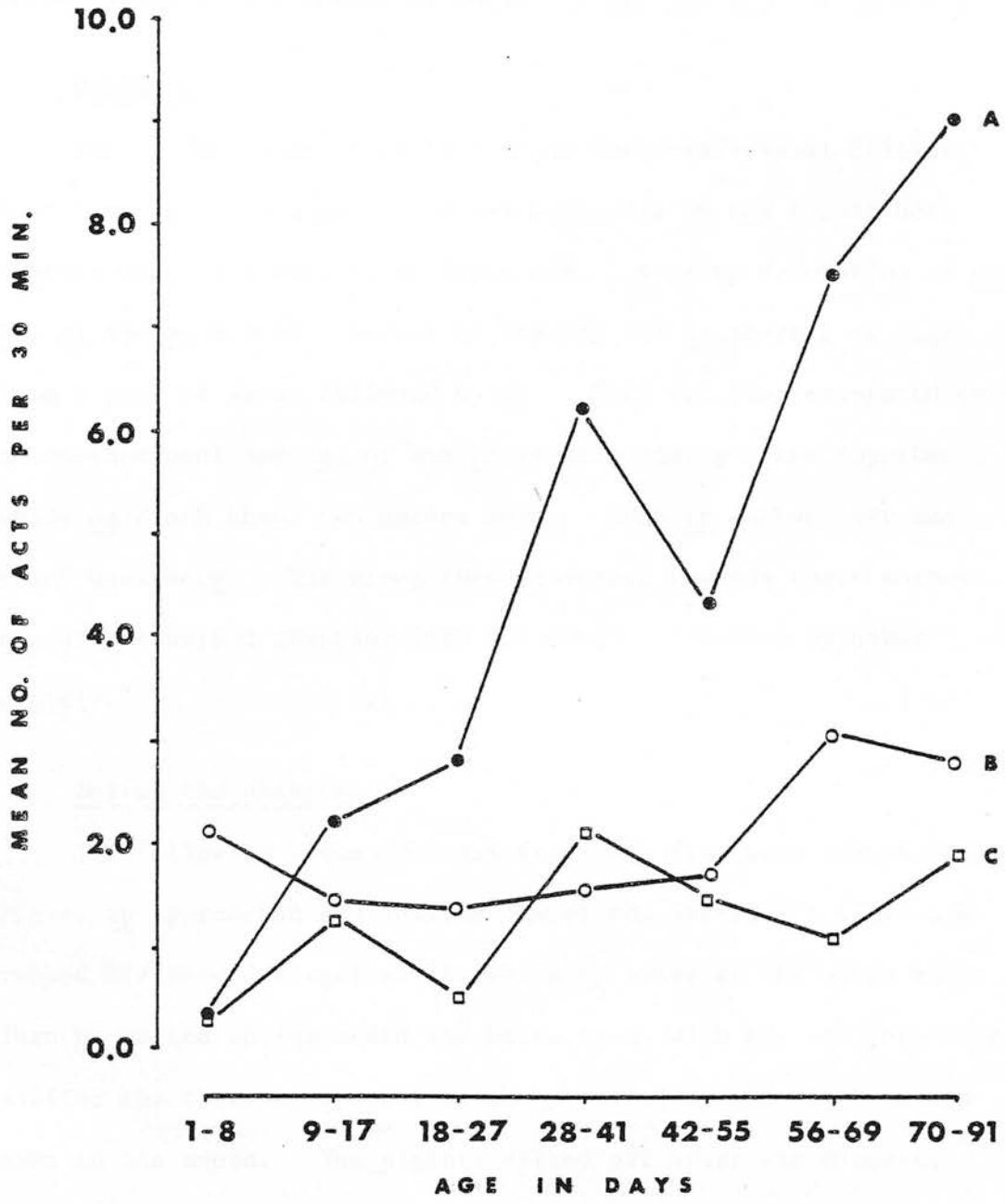

Figure 1.19 Changes in the frequency of (A) wag tail, (B) headshake and (C) rub, scratch head/body with age

hind foot and shook her head. Finally, wr and then bb rubbed their sides. Thus, this inter-individual bout of rubbing and scratching, which lasted five minutes, included 12, bp, pr, bb, pb, bg and wr.

Drinking

The following is an example of an inter-individual drinking bout lasting two minutes which was performed by the August born piglets when they were seven weeks old. A group consisting of og, ob, or and oo walked together to the bog and oo started to drink from a pool of water followed by og. They all then scampered over to another pool and oo, or and ob drank standing close together while og drank about two metres away. Then or walked over and drank beside og. The group then scampered towards their mother, RR, as she walked grunting into the woods surrounded by other piglets.

Nosing the observer

The following sequence comes from WB's five week old piglets. Piglet bp approached and sniffed one of the observer's boots and rubbed his shoulder against it, while wy nosed at the other boot. Then bo walked up and nosed the boots along with bp, and they both sniffed the observer's coat, which bp chewed at and shook up and down in his mouth. The piglets walked off after six minutes, engaged in social interaction.

Nosing unusual objects

The final example describes the behaviour of the February born piglets at one month of age, when a piece of black plastic blew into the Pig Park. Groups of piglets nosed and manipulated it on three occasions that day, each bout being separated by at least thirty

minutes. In the first bout, yr picked up the plastic in her mouth and scampered carrying it and shaking it about. Then yy, yg and by sniffed at it and blw chewed it. Now yr picked it up again and scampered together with yy, yg, blw, rb and rbl, dropping it as she ran.

Later, pb and pbl sniffed the plastic, followed by pg, bg and bb, and then by pbl, wbl and wo, who bit at it. Piglet pbl picked it up and dropped it, and then pg and wr chewed it.

In the third bout, by scampered, shaking the plastic in her mouth, and when she dropped it, wr walked up and sniffed it. Then pbl shook it, and pb followed her, sniffing at it as she carried it.

3 Results of cluster analysis

The February litters

Between birth and four weeks of age, all piglets were connected to at least one other piglet at a similarity of 167. Eighty-two per cent of the piglets were most similar to a littermate, the exceptions being bp, br, pr and wg. As with his resting associations, blw was most similar with a member of 2's litter (his adopted one). However, B_2 cluster analysis at a similarity of 167 showed that, unlike resting, most piglets belonged to the same cluster and did not form distinct clusters according to litter.

Between four and thirteen weeks, a similarity of 100 connected all piglets, and at this level all but five piglets fell into the same B_2 cluster. Social facilitation was still most likely to occur with a littermate (73.7 per cent of the piglets), with five exceptions, of whom yg, wo and wg were most similar to their mothers, blw to a former littermate from RR's litter and only pw to

an unrelated piglet. Adults were now more likely to appear in inter-individual bouts with piglets than they were at the earlier age, but juveniles rarely appeared at either age. Of all the piglets, only pbl and wbl were most similar to each other at both ages.

WB's litter

All of WB's piglets were joined together in a B_2 cluster at similarities of 227, between birth and three weeks, and 255, between three and six weeks. As with resting, bouts involving social facilitation included WB and 4 during the first age period, while in the second, when juveniles started resting and interacting with the piglets, they sometimes appeared together in bouts. However, at both ages, all of the piglets were most similar to a littermate.

The August litters

Between four and thirteen weeks of age, all of the August born piglets were connected together at a similarity of 91, and the whole group, including the adults and juveniles, fell into the same B_2 cluster at this level. Of the twenty-four piglets, seventeen (70.8 per cent) were most similar to a littermate.

V Dominance relationships

The word 'avoidance' was used to refer to all instances of turning, walking or running away from the close vicinity of another animal (i.e. within one metre). This occurred as a result of aggression received from the other animal in the form of a bite or threat. It also resulted from other types of interaction such as approaches or sniffs, and, in some cases, a small movement of the head of a more dominant animal, without any apparent aggressive intent, was sufficient to cause avoidance. When a piglet was chased away following a vigorous circle fight with biting, it could continue to retreat for several metres. However, most interactions were less intense, and a low ranking piglet avoided a more high ranking one by walking away a few steps or by turning so as to place its hindquarters between its head and that of the other pig. Often no evidence of dominance was obtained from an interaction because (a) both piglets moved away from each other at the same time, (b) both piglets remained together or (c) the piglets were interrupted by extraneous events (e.g. the sow started grunting, calling her piglets to the udder, or during a circle fight, another piglet started circling with one of the interactants). For many pairs of piglets, no observations of avoidance were made, and it is possible that some piglets avoided those of higher rank by keeping well away from them. Subtle avoidance occurring at a distance was not sampled, as it could not easily be distinguished from avoidance of other nearby piglets or from movements occurring for reasons other than avoidance.

Matrices showing the number of times which each piglet avoided each other piglet in its group are given in Figures 1.20 to 1.23.

Figure 1.20 Matrix of dominance relationships: February litters (0-4 weeks)

Give avoidance

Receive avoidance	wg	pb	wbl	pbl	wo	wr	py	pr	pw	pg	bb	bp	blw	by	br	bg	yw	yy	yr	yg	rb	rbl	yo
wg		-	3	1	4	2	4	3	2	5	3	1	-	-	-	-	-	2	-	1	-	-	-
pb	-		1	1	1	2	1	-	-	-	1	1	1	-	-	-	1	-	-	1	-	1	-
wbl	2	-		4	-	4	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
pbl	-	1	1		2	4	2	1	3	1	1	1	-	-	1	-	1	-	-	1	-	-	-
wo	-	-	-	1		5	2	1	-	2	1	-	-	1	3	-	-	-	-	-	1	-	-
wr	3	1	-	2	1		1	2	4	4	1	-	-	2	1	-	-	-	1	-	1	-	-
py	-	-	2	1	-	-		1	1	2	-	-	-	-	-	-	-	-	-	-	-	1	-
pr	-	-	-	2	-	-	-		3	2	1	1	1	-	-	1	-	1	-	1	-	3	-
pw	-	-	4	-	2	-	1	-		1	1	-	-	-	-	-	-	-	-	-	-	1	-
pg	-	-	1	-	-	-	1	-	2		4	-	-	2	2	5	-	-	-	-	1	2	-
bb	-	-	1	-	-	-	-	-	-	-		6	7	8	8	9	1	1	1	2	-	-	-
bp	-	-	1	-	3	-	-	-	-	-	1		6	3	2	6	2	5	-	2	-	3	-
blw	-	-	-	-	-	-	-	-	-	-	2	2		15	5	7	3	3	2	4	2	-	2
by	-	-	-	-	-	-	-	2	1	-	-	6	-		5	3	1	1	-	1	1	1	1
br	-	-	-	-	-	-	1	1	-	-	2	2	5	-		10	3	1	2	2	1	2	3
bg	-	-	-	-	-	-	1	-	-	-	1	-	3	4	2		3	5	5	1	1	1	-
yw	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-		2	-	1	1	2	3
yy	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-		1	2	2	2	1
yr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		1	1	-	-
yg	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	-	-		3	5	1
rb	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	1		2	2
rbl	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-		-
yo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

Per cent scores above diagonal = 81%

Figure 1.21 Matrix of dominance relationships: February litters (4-13 weeks)

Give avoidance

Receive avoidance	wbl	pb	pbl	wg	wo	pr	pw	pg	bb	by	bp	br	bg	py	blw	yg	rb	rbl	yr
wbl		3	3	2	8	3	1	4	2	1	-	3	-	4	3	1	2	-	4
pb	1		1	3	2	1	1	1	1	-	-	-	3	1	1	-	-	-	2
pbl	-	-		6	2	4	4	3	-	3	2	1	2	-	4	1	1	5	2
wg	3	1	-		12	4	-	2	6	1	3	3	1	3	6	3	3	3	3
wo	-	1	-	3		8	2	7	3	9	2	3	6	7	4	3	3	-	1
pr	-	1	1	-	3		1	6	3	5	2	2	3	2	8	-	3	4	3
pw	1	-	-	-	2	-		1	-	2	-	1	-	-	2	1	1	-	1
pg	-	1	-	-	1	-	-		5	1	2	3	2	-	3	3	5	6	3
bb	-	-	-	1	-	1	-	-		5	10	3	6	7	2	1	4	6	1
by	-	-	-	-	1	-	-	-	1		8	3	-	1	2	4	2	4	3
bp	-	-	-	-	-	-	-	1	-	1		6	1	2	5	1	4	-	2
br	1	-	-	1	-	-	-	1	1	-	-		3	3	8	2	4	4	2
bg	-	-	-	-	-	-	3	-	-	1	1	-		8	1	3	13	-	3
py	-	-	-	-	-	2	-	-	-	-	2	1	-		4	7	3	5	2
blw	-	-	1	-	-	-	1	-	-	2	-	-	3	-		6	8	7	4
yg	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		3	1	-
rb	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	3		9	-
rbl	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	3		10
yr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	

Per cent scores above diagonal = 90%

Figure 1.22 Matrix of dominance relationships: WB's June litter (0-6 weeks) with adults and juveniles

Give avoidance

Receive avoidance	7	2	4	12	RR	WB	WG	PW	PG	BP	BG	YG	RB1	YR	RB	bp	bb	bo	wy
7		-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	2	3
2	-		1	1	1	3	-	-	-	-	-	-	-	-	-	-	-	1	1
4	-	-		-	3	1	1	2	1	2	1	-	-	1	1	-	-	-	1
12	-	-	-		4	6	-	1	-	-	-	-	-	-	-	-	-	-	-
RR	-	-	-	-		6	-	-	-	1	-	-	-	-	-	-	-	-	-
WB	-	-	-	-	-		2	-	-	1	1	-	4	5	5	5	2	4	5
WG	-	-	-	-	-	-		-	-	-	-	-	-	-	-	1	1	-	-
PW	-	-	-	-	-	-	-		-	-	-	-	-	1	-	1	-	3	5
PG	-	-	-	-	-	-	-	-		-	-	-	-	-	-	1	-	1	3
PB	-	-	-	-	-	-	-	-	-		-	-	-	1	-	-	-	1	2
BG	-	-	-	-	-	-	-	-	-	-		-	-	-	1	5	-	8	7
YG	-	-	-	-	-	-	-	-	-	-	-		-	-	-	1	-	-	3
RB1	-	-	-	-	-	-	-	-	-	-	-	-		1	-	3	-	4	12
YR	-	-	-	-	-	-	-	-	-	-	-	-	-		1	3	-	8	7
RB	-	-	-	-	-	-	-	-	-	-	-	-	-	-		1	-	1	2
bp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		23	36	37
bb	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2		17	15
bo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	5		22
wy	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	5	5	

Per cent scores above diagonal = 86% (piglets only)

Figure 1.23 Matrix of dominance relationships: August litters (4-13 weeks)

Give avoidance

Receive avoidance

	so	or	nt	yw	ob	sg	oo	bb	og	bo	sw	yy	bp	sr	yp	ss	sp	op	bs	sy	bw	bg	os	yr
so		1	–	3	–	–	1	–	–	–	–	–	2	4	–	2	1	–	–	2	–	1	2	1
or	–		3	7	–	–	2	4	6	2	1	7	9	2	–	5	1	1	–	–	1	2	3	1
nt	–	1		4	3	1	1	5	3	–	–	1	2	–	–	–	–	1	–	6	1	–	–	1
yw	–	–	–		6	3	1	–	1	–	–	5	4	–	2	2	–	–	1	1	–	4	1	–
ob	2	2	–	–		3	5	6	2	1	3	1	4	–	–	6	3	3	4	4	–	–	2	6
sg	–	–	1	2	1		2	3	1	–	–	2	–	1	–	1	2	–	–	3	–	1	1	1
oo	–	–	–	–	–	1		1	–	1	–	–	3	1	–	5	2	3	1	–	–	–	–	–
bb	–	–	–	3	1	1	–		1	5	1	2	3	5	1	7	–	–	1	3	2	1	1	2
og	1	–	–	–	–	–	–	1		3	1	1	2	1	1	2	1	2	1	1	3	–	1	1
bo	–	–	–	3	–	–	–	–	1		–	10	–	1	–	4	–	–	–	–	–	1	–	2
sw	–	1	–	–	–	–	–	1	–	–		–	1	–	–	–	–	–	–	–	–	–	–	–
yy	–	–	–	–	–	–	–	2	1	–	–		5	–	1	5	3	–	2	–	1	1	2	–
bp	–	–	1	1	1	–	–	1	–	2	–	–		6	–	2	1	1	2	3	1	2	1	–
sr	–	1	–	–	–	–	–	4	–	–	–	1	2		2	5	1	–	–	4	1	–	2	–
yp	–	–	–	–	–	–	–	–	–	–	–	–	2	–		4	–	2	–	–	–	1	1	1
ss	–	–	–	2	1	–	–	–	–	–	–	1	1	–	1		1	1	3	9	–	–	3	–
sp	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	–		–	–	3	–	–	–	–
op	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	1	–		–	1	–	–	–	–
bs	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–		1	–	–	–	–
sy	–	–	–	2	–	2	–	–	1	1	–	1	–	–	–	–	–	–	–		2	–	–	1
bw	–	–	–	2	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–		1	–	–
bg	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	1
os	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–		1
yr	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	

Per cent scores above diagonal = 85%

Figure 1.22 also includes the adults and juveniles present in the Pig Park with WB's piglets. If no dominance hierarchy existed, then one would expect that the scores on a matrix would be equally divided on either side of the diagonal. However, in all cases, it was possible to arrange the piglets in a hierarchical order so that at least eighty-one per cent of the results fell above the diagonal. Piglets at the top of the hierarchy were usually avoided by those below them, although there were some triangular dominance relationships. For example, it can be seen in Figure 1.20 that bp was usually avoided by blw who was avoided by by, and yet by was avoided by bp. Figure 1.22 shows that adults were always avoided by juveniles, which were avoided by piglets.

As the data for many pairs did not give a clear indication of the direction of dominance, the results were examined using two different criteria of dominance. In the first, a piglet was considered to be the subordinate member of the pair if it was seen to avoid the other at least one more time than *vice versa*. Using this criterion, dominance relationships could be determined for fifty-seven per cent of the possible pairs of February born piglets during their first month, and this increased to eighty-two per cent between their fourth and thirteenth week. Of those pairs exhibiting dominance relationships during both periods, eighty-nine per cent of relationships remained unchanged and only eleven per cent reversed direction (i.e. the previously dominant individual became the subordinate). Dominance relationships could be determined between all pairs in WB's litter during their first six weeks (100 per cent), and between sixty per cent of the pairs born in August between their fourth and thirteenth week.

The second criterion required that the subordinate avoid the dominant member of a pair at least three times more frequently than the reverse. This had the effect of reducing the number of pairs for which the direction of dominance could be determined. For the February litters, dominance was clear between seventeen per cent of the pairs in the first age period, increasing to fifty-three per cent in the second period. Of the dominance relationships apparent at both ages, no reversals occurred. All of WB's piglets had clear dominance relationships, but only twenty per cent of the August pairs had them.

The development of dominance relationships

Dominance relationships developed between piglets when they were relatively unfamiliar. They appeared between littermates during their first two weeks, when vigorous circle fights with biting occurred. Some piglets fought more than others but the piglets presumably learned which littermates were likely to win fights with them and which were likely to lose and were able to act appropriately to avoid attacks from previous winners. After this, interactions became playful rather than aggressive, but although interactions were frequently initiated with more high ranking piglets, it should be noted that the same member of an interacting pair was likely to terminate the interaction by moving away in both serious and playful situations.

During early encounters with piglets from other litters, some fighting occurred between non-littermates. This is illustrated by observations on the early behaviour of the February litters. RR's piglets first visited 2's nest and sniffed her piglets when they

were nine days old, and fights between them were first observed three days later. Fighting continued for a week, by which time members of the two litters were well-acquainted and frequently found together. The first aggression observed with members of 12's litter occurred when RR and 2 led their piglets down to 12's nest. The piglets entered the nest and sniffed 12's udder and then all left with the exception of RR's piglet bp (who was now fourteen days old). She circled round fighting with wo, who then ran away from her (and chased and bit wr, who was subordinate to him). Then she bit wbl, who walked away, and she sniffed noses with pbl. Now she bit wo again, who squeaked and walked away, but when wg then bit her, they fought and she ran away from him and chased wo. After several more aggressive incidents (with pw, pr and wr), she lay down to rest with 12's piglets, but later left to rejoin her own group. From this set of encounters it can be seen that not all of 12's piglets interacted with bp, and of those which did, wg won a fight with her, wo lost one and subsequently avoided her, and pbl showed no obvious aggression towards her. Over the next few days, more fights occurred between 12's piglets and members of RR's and 2's litters, and by the end of the first month all piglets were familiar with each other and had probably established dominance relationships. Thus, in the first dominance matrix (Figure 1.20) most avoidances were between members of RR's and 2's litters on the one hand and between members of 12's litter on the other, whereas in the second matrix (Figure 1.21), avoidance occurred between members of all three litters. Of the avoidances resulting from acts of aggression, sixty-eight per cent (126 out of 185 acts of aggression) occurred during the first month for the February born piglets, and

ninety-four per cent (62 out of 66 aggressive acts) were observed during the first three weeks of life of WB's piglets.

Factors affecting the probability and direction of avoidance

It was interesting that social rank (i.e. position in a dominance hierarchy) was related to litter membership in the February litters, with members of 12's litter tending to be higher ranking than members of RR's litter, which were higher ranking than 2's piglets. In fact, when blw and py started suckling from 2, they seemed to drop in rank relative to some of their former littermates although remaining dominant over 2's piglets. Similarly, most of RR's August born piglets were higher ranking than their contemporaries in 2's litter. However, piglet dominance was not related to the dominance status of the dam, as 2 was avoided by 12, who was avoided by RR. (The adults had stable dominance relationships with each other, which had remained unchanged since the mixing of the gorse and forest enclosure groups in December, 1979. They could be ordered into a linear dominance hierarchy, as shown in Figure 1.22.)

The relative age, weight and size of pigs affected their dominance status when there was a large differential. For example, WB's piglets, which were born in June, remained higher ranking than 12's July born piglets for at least two months, and they were all higher in rank than the August born piglets of RR and 2 for at least three months. Juveniles were always subordinate to adults, who were aggressive towards them. Young piglets rarely received aggression from adults, but they kept out of their way, presumably because they could easily have been injured or killed if

accidentally stepped upon. As they grew older they did receive some snaps and bites from adults, but these were mainly given by their mothers during weaning. For example, the August born piglets avoided adults on thirty-eight occasions during their fourth to thirteenth week, and of these twenty-six resulted from acts of aggression. Two were delivered by RR, seventeen by 2 and seven by the other four adults. The piglets also avoided the juveniles, especially when they directed aggressive or (rough) playful behaviour towards them.

Among piglets born within a few days of one another, relative age seemed to have little influence on social rank, but there was a positive relationship between weight and social rank in most cases. For instance, although two days younger, most of 12's February born piglets were higher ranking than RR's piglets. However, they were heavier than 2's piglets, which tended to be the lowest in rank by the time that dominance relationships had developed. The mean weight per piglet in 12's litter at the end of the first month was 9.7 kg compared with 8.5 kg in RR's litter and 7.8 kg in 2's litter (see Table 1.2). Among the August born piglets, the mean weight of those in the top half of the dominance hierarchy was only slightly higher than that of those in the bottom half (4.4 kg versus 4.1 kg, during the third week; see Table 1.4). Between individuals, the dominant piglet in a dyad tended to be slightly heavier than the subordinate, but there were many exceptions (e.g. bp was dominant over blw although smaller and lighter). However, very small piglets (runts) were subordinate to all others (e.g. yo in Figure 1.20, and os and yr, in Figure 1.23, were the lightest members in their respective groups).

Although males circled, bit, pushed and shoved more frequently than females at all ages ($\chi^2 = 219.97$; d.f. = 5; $p < 0.001$), these behaviour patterns were often performed in a playful rather than aggressive manner, and there was no link between sex and dominance during early development. Males and females could be found at the top or bottom of a dominance hierarchy. Neither did the relative aggressiveness of individuals affect their position in the hierarchy. For example, the February born piglets pg and bp were the most aggressive members of their respective litters (12's and RR's) and yet were not the highest ranking members. Also, although a piglet won a fight with another early in life, this did not necessarily result in a lasting dominance relationship in that direction. As described above, after fighting with wo at the age of fourteen days, bp was avoided by him three times within fifteen minutes. However, subsequently, wo was observed to displace bp from rooting sites while foraging.

The probability of a piglet avoiding another familiar piglet without first receiving an overt act of aggression depended on the relative motivation of the two piglets to compete for a resource. If well-fed and comfortable, then some piglets avoided certain others even though they had never been observed to fight together. It is possible that they avoided aggression as a general reaction, based on previous experience with others. However, if a piglet was hungry or tired, then it was likely to remain at its foraging or resting site rather than immediately moving away upon the approach of a piglet normally avoided. Therefore, the dominance hierarchies shown in the matrices do not necessarily reflect the relative strengths and fighting abilities of the piglets, as it is likely that many pairs never actually had to compete seriously for a

resource. This idea is supported by the fact that the August litters were weaned earlier than the February litters, suggesting that competition for solid food may have been more important to them. If so, it is interesting that, between four and thirteen weeks, they showed a higher level of aggression prior to avoidance than had the February born piglets. Of 452 avoidances, twenty-five per cent involved overt aggression in the August group, whereas in the February group, 569 avoidances were observed, of which only ten per cent involved overt aggression ($\chi^2 = 17.22$; d.f. = 1; $p < 0.001$). Also, as previously mentioned, fewer clear dominance relationships were found in the August group, possibly as the piglets were less willing to avoid one another to obviate confrontation over resources.

A final factor affecting the probability and direction of avoidance in each dyad of piglets in a group was the type of activity in which the piglets were involved. Prior to the formation of strong teat preferences, a wide range of intensity occurred in competition for teats, varying from an accidental or deliberate push by one piglet resulting in the other moving along the udder to try other teats, to vigorous knocking, pushing, biting and screaming in which both piglets persevered in their competition for the same teat. When the piglets in WB's litter, which successfully defended or displaced others from teats during the first four days, were compared with those avoided away from the udder during this period, differences were found. For example, whereas bp was avoided away from the udder by all three littermates at least three times more than *vice versa*, at the udder he was only observed to participate in one dispute, in which wy successfully defended a teat from him.

Once strong teat preferences were formed, piglets defended their teats vigorously and did not avoid those who might be avoided away from the udder.

Although uncommon during early development, mounting, when it occurred, usually resulted in avoidance by the receiver. During the first month, the piglets observed to mount were in all cases dominant over the receiver in other situations. However, in older piglets this was not always the case. Therefore, mounting may be linked with the exertion of dominance on some occasions.

Finally, as the piglets were obtaining most of their food requirements from milk during their first month, and as adequate creep food was supplied, spread out in troughs and on the ground, high levels of aggression were not observed at the feeding site. The probability of avoiding another piglet is likely to have been affected, partly, by the relative degree of hunger of the piglets, which would vary with time after feeding and suckling, and partly by the availability of food elsewhere. However, where a piglet was observed to avoid another at least three times more than *vice versa* away from the feeding site, it was also likely to do so while feeding on creep food.

Most of the observations of avoidance observed away from the feeding site after the first month involved displacements from rooting sites, although the displacer often did not remain to root in its new location. Therefore, the dominance relationships shown in Figures 1.20 to 1.23 probably indicated potential priority of access to food resources, which presumably became more important with age and did not necessarily provide the dominant member of a pair with a great advantage during early life. Dominance was not

a unitary variable in piglets, giving priority of access to high ranking piglets in all situations.

VI Focal Animal Samples

1 Nearest neighbours

If subordinate individuals were avoiding dominant ones from a distance, one would expect that they would rarely have been recorded as nearest neighbours. The maximum spanning trees shown in Figures 1.24 to 1.27 illustrate the similarities between the sows and piglets for nearest neighbourship. The juveniles and other adults were avoided, as mentioned in the section on dominance, and therefore their similarities with piglets were low and they were omitted from the maximum spanning trees. Of the piglets, most (76 to 100 per cent) were most likely to have a littermate as their nearest neighbour. However, non-littermates also acted as nearest neighbours on some occasions, and there was no evidence that subordinates were keeping well away from dominants, probably because avoidance could occur while foraging in close proximity by facing away from a more dominant individual. An analysis of the relative orientations of different animals, and of the absolute distances between them would probably have been more profitable for determining the effect of dominance on the distribution of individuals within an area.

Concerning the development of proximity of piglets to different categories of pig, the members of each litter remained within five metres of their farrowing nest during their first few days, making short forays out of the nest while staying within one to two metres of other piglets. The sows first went for food at the artificial feeding site between one and six days after farrowing, and the piglets first followed them there between five and thirteen days of age. They now also followed their mother to other areas of the Pig

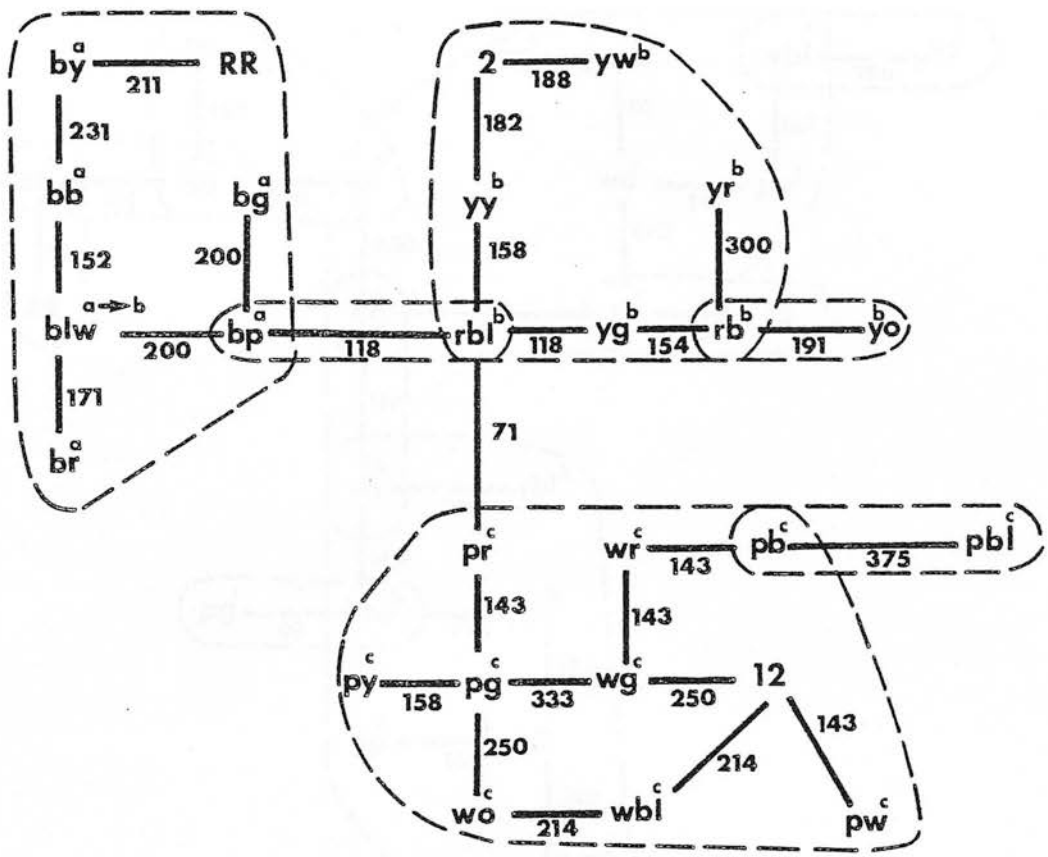

Figure 1.24 Nearest neighbours of the February born piglets; 0-4 weeks. Mean number of scans per piglet - 11.2; Numbers - similarities; Solid lines - maximum spanning tree; Dotted lines - B_2 clusters at a similarity of 118; a, b, c - piglets of RR, 2 and 12 respectively; blw switched litters during this period.

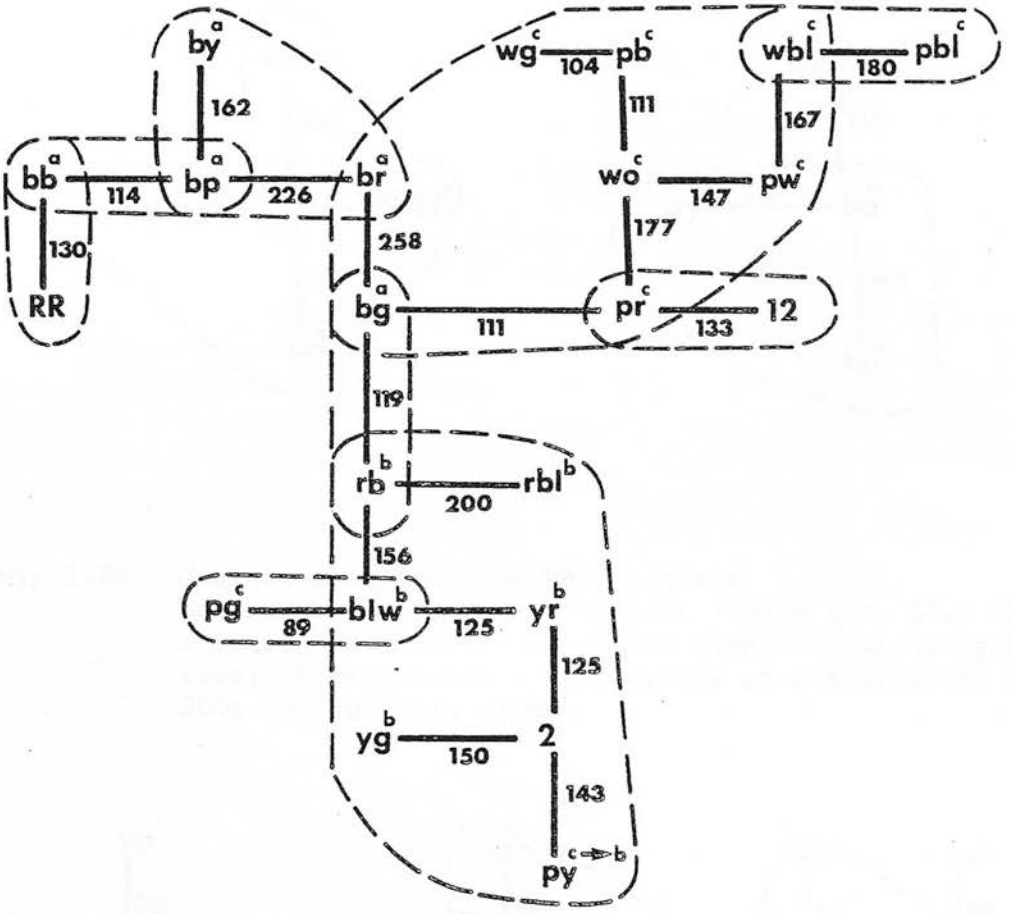

Figure 1.25 Nearest neighbours of the February born piglets; 4-13 weeks
Mean number of scans per piglet - 19.7; Numbers - similarities; solid lines - maximum spanning tree; Dotted lines - B_2 clusters at a similarity of 89; a, b, c - piglets of RR, 2 and 12 respectively; py switched litters during this period.

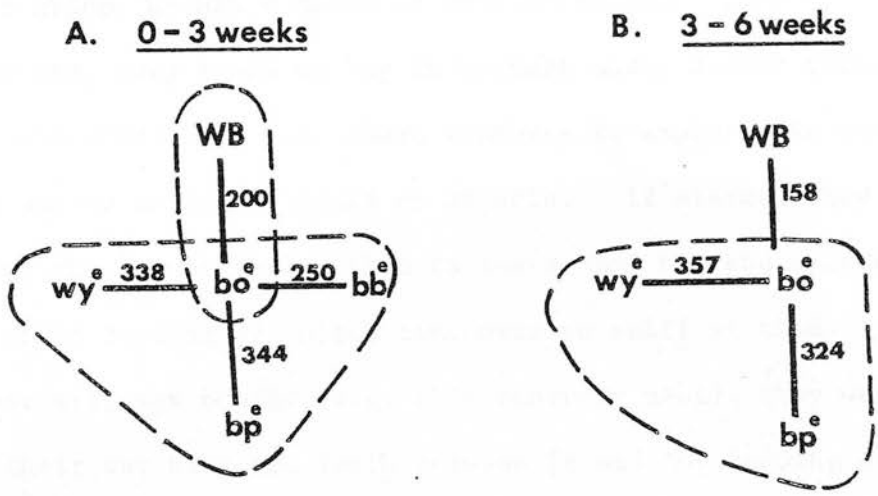

Figure 1.26 Nearest neighbours of WB's piglets
Mean number of scans per piglet - 34.0 (A), 33.3 (B); Numbers - similarities; Solid lines - maximum spanning tree; Dotted lines - B_2 clusters at a similarity of 200; e - piglets of WB.

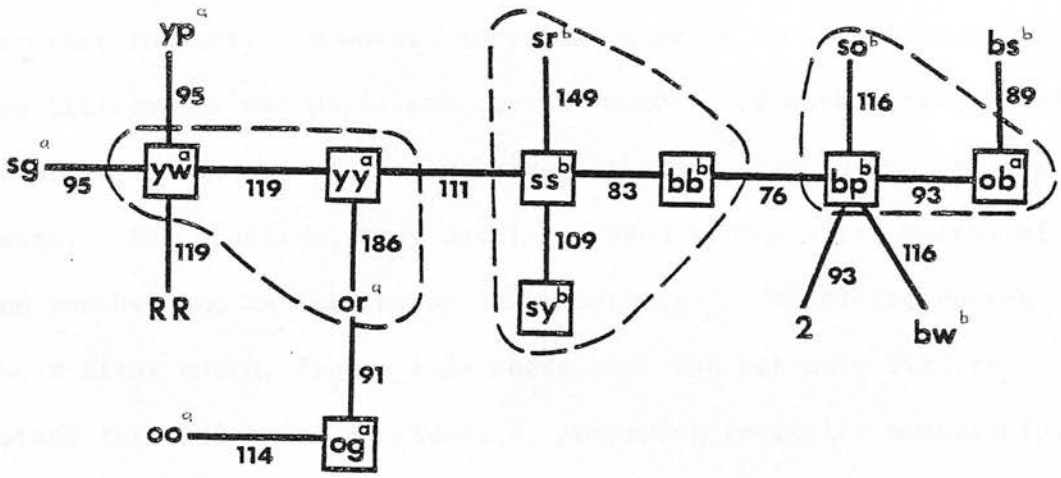

Figure 1.27 Nearest neighbours of the August born focal piglets (in boxes); 4-13 weeks
Mean number of scans per piglet - 47.3; Numbers - similarities; Solid lines - maximum spanning tree; Dotted lines - B_2 clusters at a similarity of 76; a, b - piglets of RR and 2 respectively

Park, such as foraging and drinking sites. The sow encouraged them to follow her with frequently repeated grunts, and they all moved in a compact group, within a metre of each other (see Plate 4). While their dam fed, they stood or lay in contact under nearby gorse bushes, from where they made short ventures to explore the surrounding area and to sniff and mouth at objects. If alarmed they ran back under the bushes rather than to their dam, but she grunted frequently while feeding and often came over to sniff at them. If their nest site was nearby (e.g. RR's February nest), they were able to find their way back and forth between it and the feeding site, whereas if it was distant (e.g. 12's February nest, WB's June nest) they waited until their dam had finished feeding before returning with her to the nest.

During their second to fourth week, the piglets became more familiar with their physical and social environment. They usually travelled in groups with littermates, and returned to the nest together to rest. However, they also started to associate with non-littermates and while some or all members of each litter moved together, in groups of varying size, others rested in one or more nests. While active, they usually stayed within three metres of one another and ten metres of their mothers. Therefore, during their first month, Figure 1.24 shows that the February litters formed three distinct B_2 clusters, according to litter membership. (Most of the scans made of blw's nearest neighbours were made before he switched to 2's udder, and so he was most similar to members of RR's litter.) WB's litter (Figure 1.26) formed a group distinct from others during their first six weeks, and rarely associated with 12's July litter, while active, until those piglets

Plate 4 A sow calls her four day old piglets to her with soft, rapidly repeated grunts. They have been standing in a close huddle under a gorse bush while she has been foraging in the open

were over two weeks old. Also, although resting with Sow 4 as well as WB during their first month, they did not maintain close proximity to 4 outside the nest.

Between four and thirteen weeks of age the piglets became more independent of their dams and sometimes missed sucklings because they were elsewhere, while other members of their litter were following their mother, demanding to be suckled. In order to be present at sucklings, it was obviously of importance for the piglets to be aware of the location of their mother, and to approach her at times when she was likely to suckle them. This common attraction towards their mother resulted in close proximity to littermates and the sow during this period, and as py and blw now suckled from 2, they were now most similar to 2 and her piglets (Figure 1.25). It should be noted that nearest neighbour data was only collected for eight focal piglets in the August group, and so similarities between other members of that group could not be determined.

The low similarities obtained between piglets in large groups (February and August litters) as opposed to small ones (WB's litter) indicate that when piglets had a large choice of potential nearest neighbours they did not show a strong preference for one particular individual with whom they spent all of their active time. In addition, the animal most similar to each piglet at an early age was, in most cases, different from the one most preferred at a later age. Nevertheless, Table 1.12 shows that piglets were definitely more likely to be found near age-mates than older animals, and near littermates than non-littermates. If piglets were distributed at random throughout the pig group, then one would expect that their proximity to members of different classes of animal would be related

Table 1.12 The distribution of nearest neighbours between different classes of pig

Sow	Litter	Age period (weeks)	Per cent scans in which different classes of pig were nearest neighbours of focal piglet (n = number of pigs in each class)								Total No. of scans
			Littermates		Non-littermates		Mother[a]	Other adults		Juveniles	
			%	%/n	%	%/n	%	%	%/n	%	%/n
RR	February	0- 4	75.0	15.0[b]	8.7	0.5	11.5	1.0	0.2	3.9	0.4	104
2	February	0- 4	50.7	8.5	32.4	2.0	11.3	1.4	0.3	4.2	0.4	71
12	February	0- 4	73.5	8.2	12.1	0.9	10.8	0.0	0.0	3.6	0.4	83
RR	February	4-13	40.0	10.0	42.9	3.1	5.5	8.8	1.8	3.3	0.3	91
2	February	4-13	41.3	8.3	40.5	3.1	7.9	5.6	1.1	4.8	0.5	126
12	February	4-13	52.2	7.5	35.7	3.3	4.5	5.1	1.0	2.6	0.3	157
WB	June	0- 3	81.6	27.2	none available		14.7	2.2	0.4	1.5	0.2	136
WB	June	3- 6	62.8	31.4	2.9	1.5	11.8	3.9	0.8	18.6	2.1	102
RR	August	4-13	42.7	4.3	29.2	2.3	7.0	11.9	2.4	9.2	1.8	185
2	August	4-13	55.4	4.6	26.9	2.5	6.2	3.1	0.6	5.2	1.0	193

[a] As piglets have only one mother, a column for % scans ÷ no. of animals in this class is unnecessary

[b] This shows that, of 104 scans on RR's six piglets, a littermate was the nearest neighbour in 75% of them. As five littermates were available to act as nearest neighbours, the mean per cent of scans per littermate was 15%

to the relative availability of these animals. Yet, division of the results in Table 1.12 by the number of animals in each class demonstrates that the piglets were showing preferences for littermates and their mother over non-littermates, other adults and juveniles.

2 Social interactions

Frequencies

Figures 1.28 and 1.29 illustrate changes in the mean frequencies of some social behaviour patterns with age. (A complete list can be found in Appendix B.2.) As mentioned in the section on dominance relationships, circle fights with biting were most common during the first two to three weeks. After this, bites were inhibited. (They did not lacerate the skin, and were often performed without making contact with the body.) Whereas biting declined in frequency with age, circling increased to a peak during the fourth to sixth week, when it occurred in a playful, rather than serious, context. That is, the same movements were performed but without fierce biting and chasing. Instead, a contest of strength occurred, with the two piglets pushing at each other's shoulders. Pushing and shoving were also common during this period, especially during play, but dropped in frequency at the start of weaning (forty-two to fifty-five days), along with circling. After weaning, they were performed during foraging bouts in order to displace others from their rooting sites.

The frequency of knocking did not vary greatly with age, but was highest during feeding on artificially supplied food and during the formation of resting huddles. Although performed as a threat, the receiver did not necessarily respond with avoidance, but might remain where it was or reply with a knock. Sometimes, the animal giving the knock immediately turned away from the receiver.

Sniffing and nosing at the head or body of another was common during the second and third weeks, and also during weaning. As well as being performed with other piglets, it was often directed

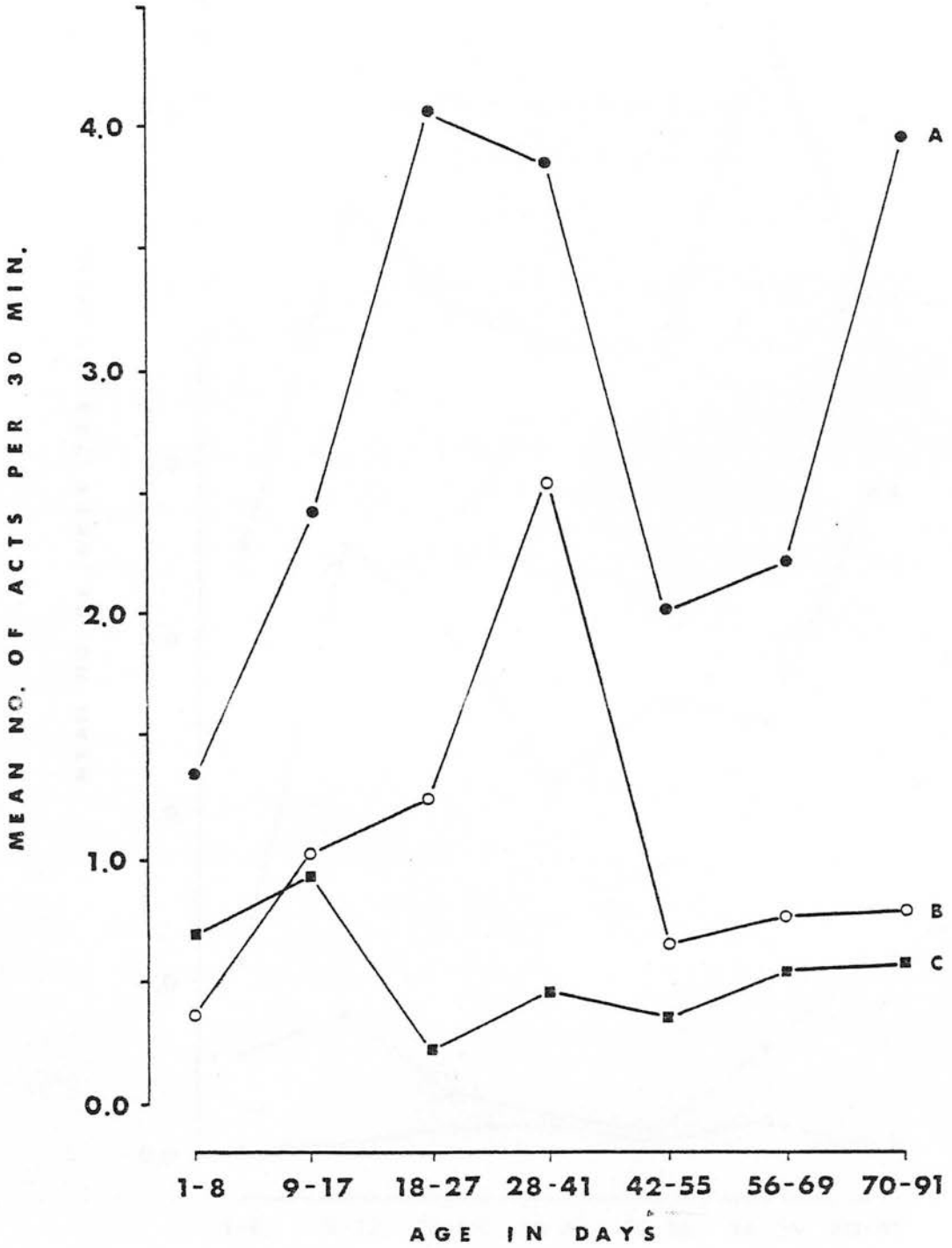

Figure 1.28 Changes in the frequency of (A) shove head/body, push heads parallel, bump, (B) circle, push heads opposing and (C) bite with age

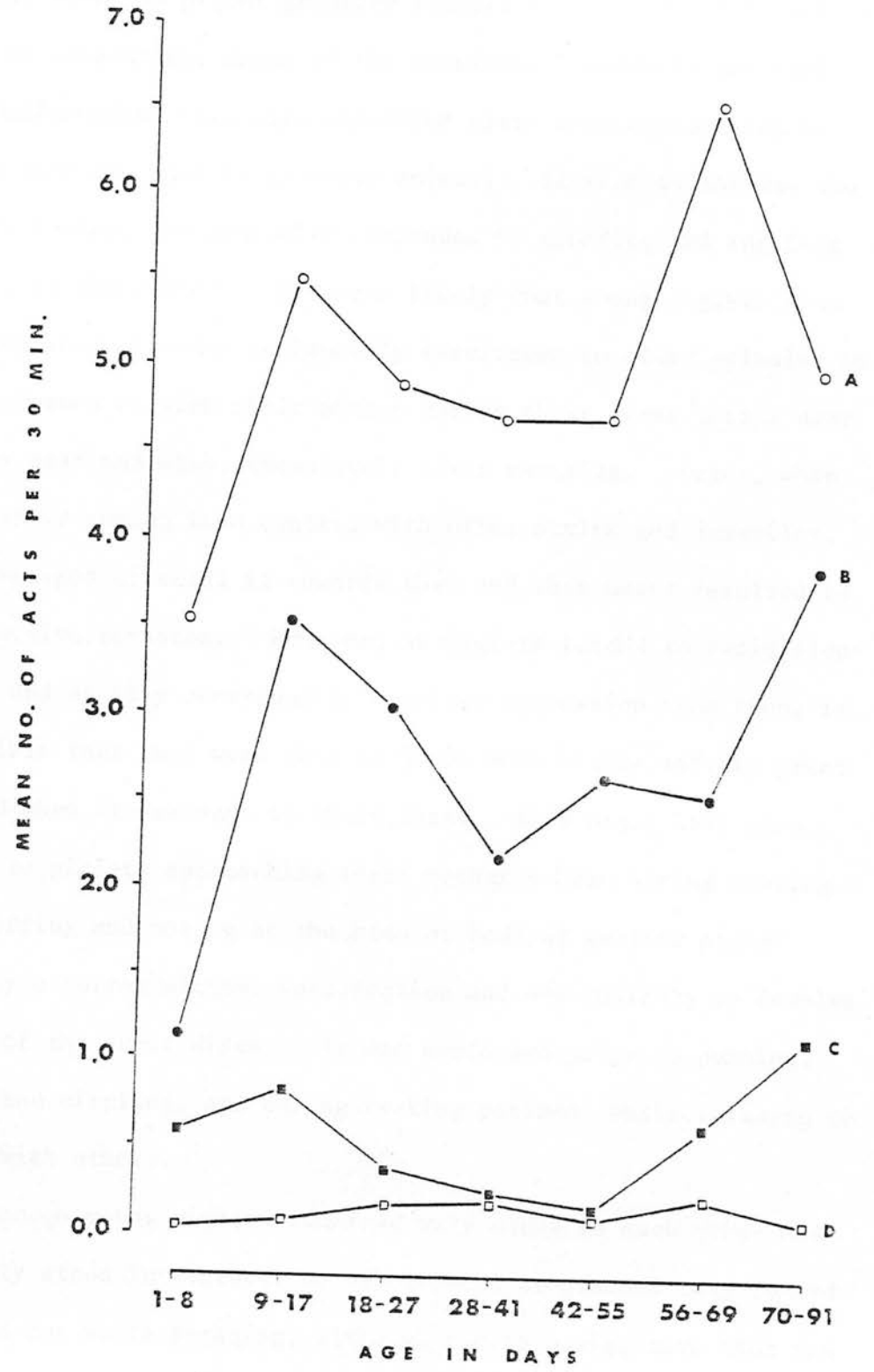

Figure 1.29 Changes in the frequency of (A) sniff noses/ head/body, (B) turn away, (C) chew head/body and (D) anogenital sniff, mount, attempt to mount with age

towards adults, especially the mother, when it took the form of a greeting, with the piglet grunting rapidly or quacking while sniffing at or towards the snout of the receiver. Quacking and rapid, soft vocalizations were also sometimes given when approaching or walking past the head of an older animal. If that animal was the piglet's mother, she generally responded by grunting and sniffing the body of the piglet. It seems likely that young piglets used this behaviour in order to identify themselves to older animals, as they performed it with their mother during their first forays away from the nest and also, immediately after suckling. Later, when they started coming into contact with other adults and juveniles, they sometimes directed it towards them and this never resulted in an aggressive response. However, as piglets tended to avoid older animals and as they occasionally received aggression from them, it is possible that they were able to judge when it was safe to greet them and when it was best to avoid them. This might have also applied to piglets approaching their mother's head during weaning.

Sniffing and nosing at the head or body of another piglet generally occurred without vocalization and was unlikely to involve contact of the snout discs. It was performed prior to pushing, shoving and circling, and during resting periods, while relaxing in contact with others.

Although young piglets remained very close to each other and frequently stood in contact, as development progressed they tended to spread out while foraging, although rarely moving more than ten metres away from other pigs. As the time spent in physical contact decreased, the frequency of close orientation of the head towards others (i.e. within one metre but not touching) increased. This

possibly reflects an increase in the subtlety of communication, which could now occur by means of eye contact and small movements of the head.

Turning away from others was most common during the first three weeks, occurring in order to avoid interactions, aggression and injury. It decreased in frequency at the time when playful circling, pushing and shoving was most prevalent (eighteen to forty-one days), but increased after weaning, as competition for solid food became more important.

Sucking and chewing at the body of others was directed by young piglets towards the ears, hair and tail of their mother, and other adults and juveniles, as they lay resting in the nest or outside in the sun. It first appeared as a form of exploration, at a time when all types of object were being chewed and manipulated, but soon became more boisterous and playful in character, as the piglets shook their mother's ears with lateral movements of the head, and clambered on her back. They also occasionally sucked the ears of their littermates in a relaxed manner as they rested together in a huddle, but if their mother's udder was exposed, they would suck and hold their teats in preference to the ears (and other parts of the body) of other piglets. An increase in the frequency of sucking and chewing occurred during and after weaning, but the actual time spent in this type of activity remained low (see Appendix B.2). This is in contrast to the high levels of non-nutritive suckling behaviour observed in early weaned piglets (see Part 2).

Sexual elements were rare throughout the suckling period, and did not appear to have a sexual motivation. A piglet might follow other piglets attempting to mount them on several occasions, on one

day, followed by days when no mounts were observed. Mounting occurred from all orientations, although no mounting from the rear was recorded during focal sampling. In all, forty-six mounts, and attempted mounts, were performed during focal animal observations, of which thirteen were directed by males towards other males and eighteen were directed by males towards females (i.e. mounting partners were not chosen according to sex to any significant extent). In addition, male adults and juveniles placed their chins on the backs of piglets (the first stage in a mounting sequence) on ten occasions. Anogenital sniffing was rare, and occurred incidentally when brief attention was paid to a tail or to a sow's vulva (when looking for teats), and when the adult's urine was, very occasionally, sniffed, no flehmen was observed. Other features of adult sexual behaviour did not appear until the animals were fourteen or more weeks old (e.g. courting grunts, pelvic thrusts, intromission). Adults occasionally sniffed at the urine of young piglets during or just after urination, and it is possible that they were interested in hormones present in the urine. No eating of the faeces of piglets by adults was observed, although this has been reported by Whatson and Bertram (1983) in intensively housed sows.

Pushing, shoving and circling associations

Although the majority of these types of interaction occurred between piglets (1,346 interactions), some shoving was directed towards piglets by juveniles (28 interactions) and adults (11 interactions), mainly in a playful context. The piglets rarely shoved at adults (4 times) or juveniles (2 times) and never circled with them, as the mutual pushing of heads and shoulders was impossible between animals of such disparate size.

Cluster analysis showed that only three of the nineteen February born piglets were most similar to the same animal during two successive age periods (0-4 weeks versus 4-13 weeks). However, littermates were preferred over non-littermates at all ages (see Table 1.13). Certain pairs of piglets developed relatively strong pushing, shoving and circling associations as they grew older (e.g. February born piglet rb1 with littermates rb and py, and WB's piglet bp with littermate bo). No discrimination was shown between the sexes during the first three to four weeks, but after this, the males of both WB's litter and the February litters pushed, shoved and circled significantly more often with each other than expected on the basis of the relative availability of male-male dyads versus male-female and female-female dyads ($\chi^2 = 247.83$; d.f. = 3; $p < 0.001$). However, in the August litters, male-male interactions were less common ($\chi^2 = 4.84$; d.f. = 1; $p < 0.05$), and male-female interactions more common ($\chi^2 = 10.93$; d.f. = 1; $p < 0.001$) than expected.

Sniffing associations

Cluster analysis was performed to determine which animals were most likely to orient towards, sniff and nose each focal piglet and *vice versa* (see Table 1.13). Comparing the associations of the February born piglets between 0 to 4 weeks and 4 to 13 weeks, only yg was most similar to the same animal (her mother, 2) at both ages. Littermates were less often connected to each other by this measure of sociality than by others, and were linked to adults and juveniles at higher levels of similarity. This suggests that sniffing was important in the formation and maintenance of social bonds with all members of the social group. Of 2,714 interactions involving sniffing, 344 were performed with the piglets' own mothers, 286 with other adults, 336 with juveniles and 1,748 with each other.

Table 1.13 Results of cluster analysis of pushing, shoving and circling interactions and sniffing interactions

Measure of sociality	Piglet group	No. of focal piglets	Age period (weeks)	Per cent focal piglets most similar to different classes of pig				
				Littermates	Non-littermates	Own mother	Other adults	Juveniles
Pushing, shoving and circling associations	February litters	23	0- 4	82.6	17.4	0	0	0
		19	4-13	94.7	5.3	0	0	0
	WB's litter	4	0- 3	100	none available	0	0	0
		3	3- 6	100	0	0	0	0
	August litters	8	4-13	75.0	25.0	0	0	0
Sniffing associations	February litters	23	0- 4	30.4	4.4	41.3	8.7	15.2
		19	4-13	47.4	15.8	15.8	15.8	5.3
	WB's litter	4	0- 3	50.0	none available	50.0	0	0
		3	3- 6	100	0	0	0	0
	August litters	8	4-13	56.3	33.3	6.3	4.1	0

3 Social relationships

If certain animals developed strong social relationships with each other, then one would expect them to be closely associated during a variety of activities. Therefore, sociograms were drawn connecting each focal piglet to the animal(s) to whom it was most similar by each of the following measures of sociality: (a) resting partners, (b) nearest neighbours, (c) co-participants in socially-facilitated bouts of rubbing and scratching, drinking, nosing unusual objects and nosing the observer, (d) pushing, shoving and circling partners and (e) sniffing partners. The number of lines connecting each pair of animals on a sociogram was an indication of the strength of their social relationship. If, for one of the measures, a piglet was most similar to another, and the other was also most similar to it, then two lines were drawn between them, and if the same was true for the other four measures, then they would be connected by a maximum of ten lines. Arrowheads were used to indicate the direction of preference in cases where one animal was most similar to another but the reverse was not true. (The word 'preference' is used here in a descriptive sense and does not imply conscious selection of social partners.) As focal samples were not made of the adults, juveniles and some of the August born piglets, it was not known to whom they were most similar, and therefore no arrows were drawn from them towards a focal piglet.

The sociograms are illustrated in Figures 1.30 to 1.33. The social relationships of different piglets varied in strength, with some piglets being connected to a different animal by each measure of sociality, while others had more than one arrow to the same animal. For example, in Figure 1.30, by had an arrow to each of

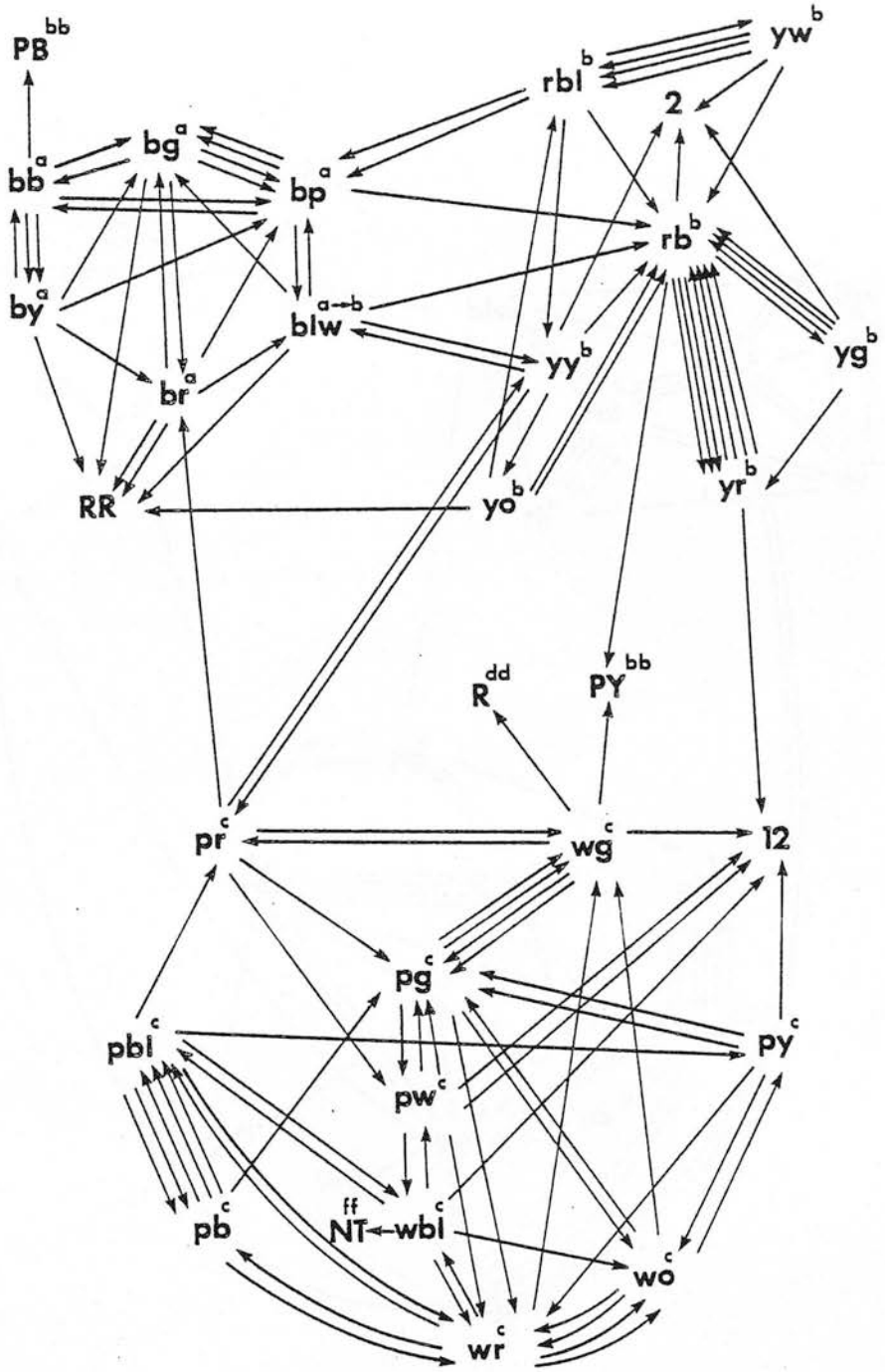

Figure 1.30 Sociogram indicating the relative strengths of social relationships among the February born piglets and other members of the Pig Park group; 0-4 weeks Arrows show animal(s) most similar to each focal piglet for five measures of sociality (resting, nearest neighbours, social facilitation, pushing and sniffing). a, b, c - piglets of RR, 2 and 12 respectively; bb, dd, ff - juvenile offspring of 2, 4 and OY respectively; blw switched litters during this period.

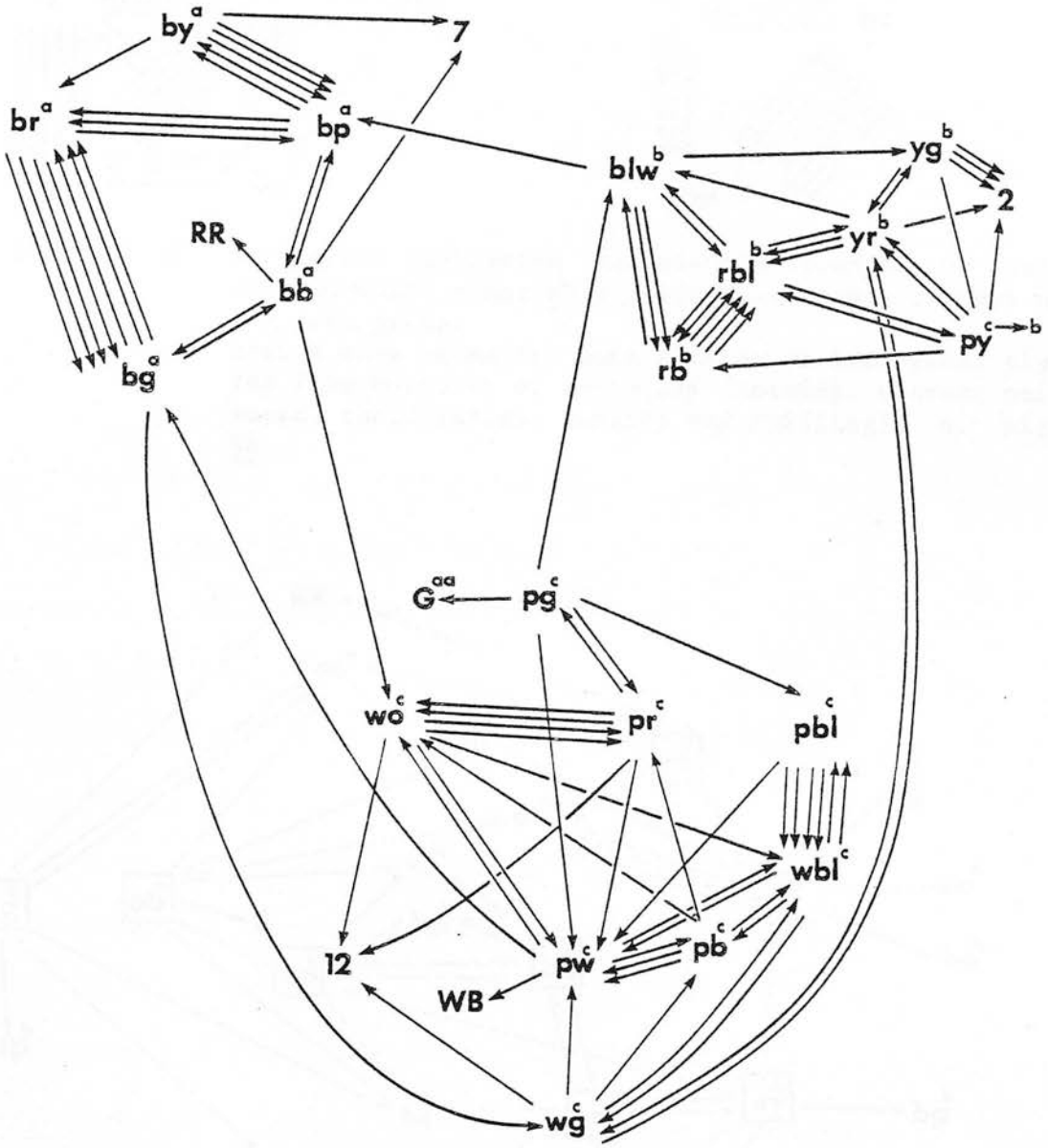

Figure 1.31 Sociogram indicating the relative strengths of social relationships among the February born piglets and other members of the Pig Park group; 4-13 weeks
Arrows show animal(s) most similar to each focal piglet for five measures of sociality (resting, nearest neighbours, social facilitation, pushing and sniffing) a, b, c - piglets of RR, 2 and 12 respectively; aa - juvenile offspring of RR; py switched litters during this period.

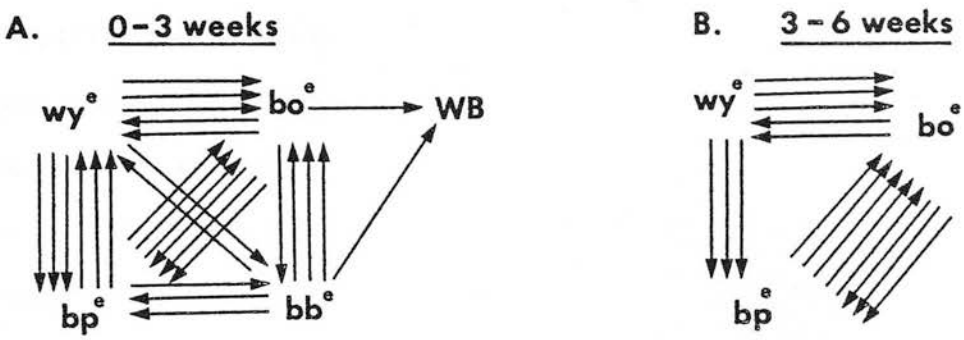

Figure 1.32 Sociograms indicating the relative strengths of social relationships among WB's piglets and other members of the Pig Park group.
Arrows show animal(s) most similar to each focal piglet for five measures of sociality (resting, nearest neighbours, social facilitation, pushing and sniffing); e - piglets of WB

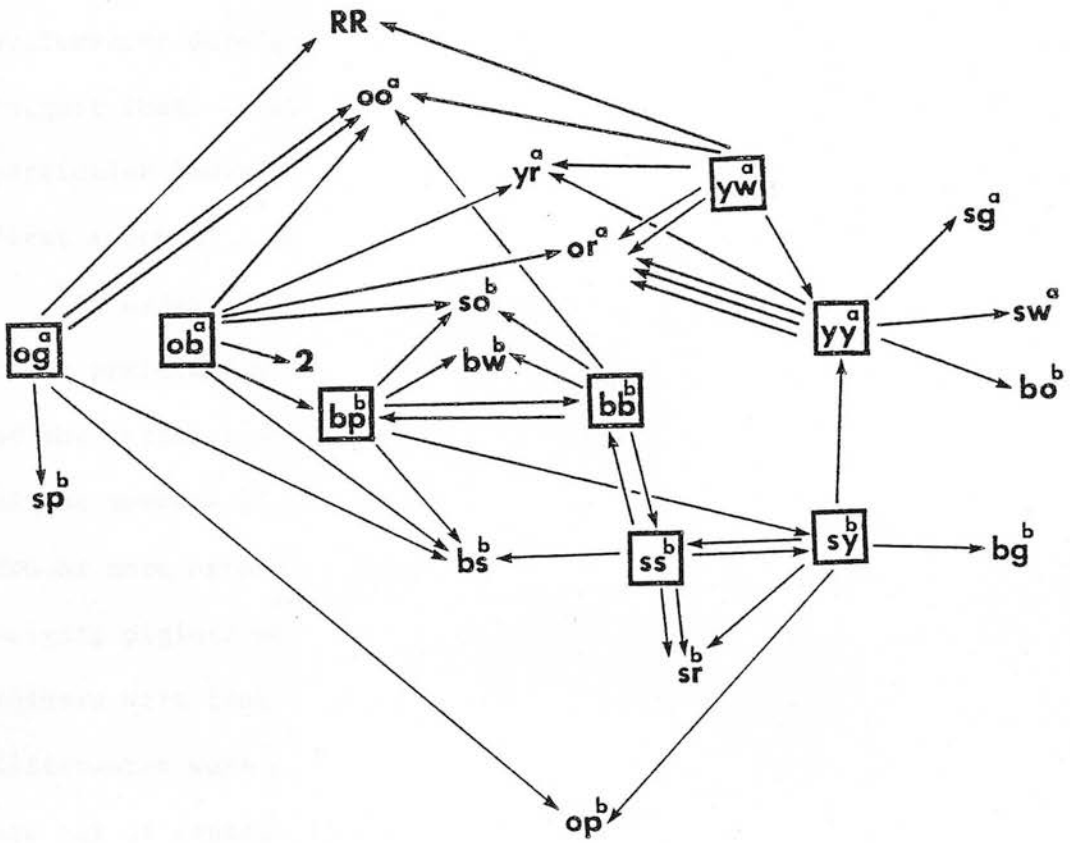

Figure 1.33 Sociogram indicating relative strengths of social relationships among the August born focal piglets (in boxes) and other members of the Pig Park group; 4-13 weeks
Arrows show animal(s) most similar to each focal piglet for five measures of sociality (resting, nearest neighbours, social facilitation, pushing and sniffing); a, b - piglets of RR and 2 respectively.

bb, bg, bp, br and RR, while yr had four arrows to rb and one to 12. Comparing relationships over time, none of the February born piglets were connected to the same animals by two or more arrows during two successive age periods. As WB's piglets had a smaller choice of potential social partners, and as they always rested together during their first three weeks (giving each pair the same similarity value for resting), they are connected to each other by more arrows than piglets in the other sociograms. However, it is evident that bp developed a stronger social relationship with his brother, bo, than with his sister, wy, between three and six weeks of age. Of the August born piglets, four of the eight focal animals were connected to the same animal by two or more measures of sociality, but their preferences during their first month were not known. The results suggest that, in general, strong lasting social relationships with particular individuals were not developed by piglets during their first month of life.

In order to determine what factors might be involved in creating preferences for particular individuals, a comparison was made of the relative age, sex, weight, dominance status and teat position of the members of each pair of piglets connected on a sociogram by two or more arrows in the same direction. Concerning age, sex and weight, piglets were preferred over adults and juveniles, and only mothers were linked to individual piglets by more than one arrow. Littermates were preferred over non-littermates at all ages, but sex was not of general importance. Neither were piglets always most likely to prefer peers of a similar weight to themselves. Figure 1.31 shows that pbl and wbl both preferred each other over other piglets, and yet the difference in weight between them at

eleven weeks was six kilograms. On the other hand, pr and wo, who had a similar relationship, differed in weight by only one kilogram. (The maximum weight difference between two piglets at this age was 15 kg, between pbl and yr.)

Relative dominance status was correlated with preferences for particular piglets in most cases after the first month. Figure 1.31 shows that fifteen of the nineteen February born piglets had relatively strong social relationships with other piglets (i.e. they were connected on a sociogram by two or more arrows to the same animal). Of these, thirteen were within two places of their preferred partner in the dominance hierarchy (see Figure 1.21). However, during the first month, only nine of the seventeen strongly associated piglets were as close in rank to their preferred partner (Figure 1.20). Of the August born focal piglets, three of the four with relatively strong social relationships were also close in social rank.

Finally, position in the teat order seemed to have little effect in determining preferences. Some strongly associated piglets were adjacent in the teat order (either vertically or horizontally) while others were spread out along the udder. For instance, in RR's February litter, br and bg suckled from R2 and R3, respectively, during their fourth to thirteenth week, while bp and by, who also had a relatively strong social relationship during this period, suckled from L1 and R5, respectively (see Table 1.7).

If littermates were associating with each other mainly as a result of their common attraction towards their mother, one might expect that, as they grew older, those who missed sucklings relatively often would have relatively strong relationships with one

another, as would those who rarely missed sucklings. However, this was not the case. Of the February born piglets over one month of age, four piglets missed seven or more sucklings (pbl, pg, pw and wbl), of whom only pbl and wbl had a relatively strong social relationship. Two piglets missed less than two sucklings (rb and py), but they did not have a strong social relationship. None of WB's piglets missed more than one suckling during their first six weeks. Also, none of the August born piglets missed more than six observed sucklings, and twelve of them missed fewer than two. Of these, only two pairs had relatively strong relationships (yw with or, and yy with or). Therefore, littermate associations did not appear to be based on the relative time spent in the vicinity of the sow.

Certain piglets appeared to be more sociable than others, in that they had many arrows pointing towards them on a sociogram while others had few. On the first sociogram (Figure 1.30), the maximum number of arrows pointing to an individual (rb) was fourteen and the minimum was one (yg, yw, yo). However, rb's early sociality did not persist into the second age period (Figure 1.31), and factors such as relative age, sex, weight, dominance and teat position were not consistently correlated with the relative sociability of individual piglets. As expected, the strength of social relationships with the mother sows decreased with age in most cases.

It is concluded that piglets formed relatively strong social relationships with littermates, but individual preferences within the litter were variable and probably of little importance at this stage in development. All littermates were well-integrated with each other and to a lesser extent with all other members of the

social group.

4 Playful versus non-playful behaviour

Frequencies

Figure 1.34 illustrates the frequencies of various behaviour patterns associated with play. The behaviour patterns scampering, hopping, pivoting, head tossing and flopping, which were chosen to be play markers because, unlike other behaviour patterns, they always occurred in a playful context, showed a combined peak in frequency between eighteen and twenty-seven days, as did trotting and galloping, and standing or crouching in an alert manner. However, examination of the age period at which each individual play marker reached its highest frequency showed that hopping and tossing the head reached a peak between nine and seventeen days, scampering, pivoting and bumping into the body peaked between eighteen and twenty-seven days, and flopping and shaking objects were rare but showed small peaks between fifty-six and sixty-nine days (see Appendix B.2). This suggests that play in piglets does not form a unitary category of behaviour.

Behaviour patterns performed significantly more and less often in association with play markers than expected from the overall ratio of play to non-play are presented in Table 1.14. With the exception of the play markers (by definition), all of the behaviour patterns performed during play also occurred in non-play, in the motivational contexts of escape (rapid locomotion, barks, alert postures), comfort (wagging the tail, rubbing, scratching) and aggression (circling, pushing and shoving). The play markers were also similar to behaviour patterns performed in non-play by piglets

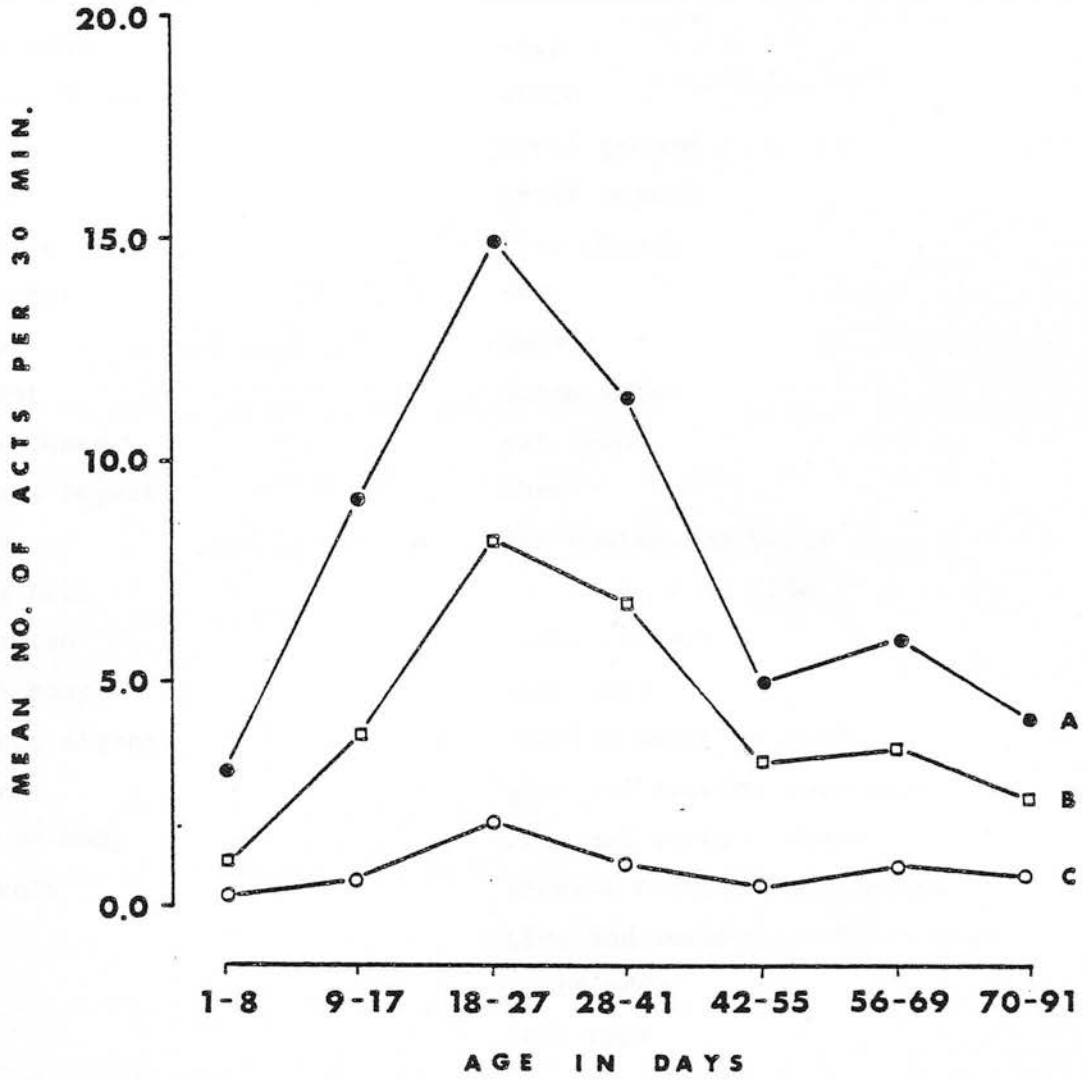

Figure 1.34 Changes in the frequency of (A) scamper, hop, pivot, toss head, flop, (B) trot, gallop and (C) alert stance with age

Table 1.14 Behaviour patterns significantly likely to be performed or received during play and non-play bouts in the Pig Park ($p < 0.05$)*

Play	Non-play
sit apart	step
stand apart	whine
walk	sniff ground
trot	sniff object
gallop	bite object
scamper	root
hop	shovel
pivot	drink water
toss head	eat food
shake object	chew
bump	lie contact on belly
wag tail	lie contact on side
scratch	stand contact
rub body	push past
alert stance	receive shove at head
bark	give and receive turn away
shove body	give and receive chase
circle	receive orientation towards
	give and receive sniff at head
	sniff udder
	suck teat

* The ratio of play to non-play was based on the total number of behavioural acts performed in sequences of play and non-play. The data for each behaviour pattern was tested in turn by the chi-squared test with one degree of freedom, after collapsing the data from all other behaviour patterns into a 2 x 2 contingency table.

or older animals (e.g. scampering, hopping and pivoting were similar to movements seen in alarm and escape, and shaking objects was similar to the shaking of live prey performed occasionally by adults). Not all of the behaviour patterns listed as occurring in play were significantly associated with play at all ages. For instance, wagging, rubbing and scratching did not appear frequently in play until after the first week. Although mounting and carrying did not occur frequently enough to be significantly associated with play, they were sometimes performed during play bouts.

Barking and alert postures appeared to be motivated by fear to start with but became incorporated into play sequences once the piglets reached eighteen to twenty-seven days of age. After this, a sudden startling stimulus sometimes elicited these behaviour patterns, which were then followed by play, while on other occasions, they were performed during an ongoing play bout apparently in order to encourage others to scamper rather than as a response to an external stimulus. It is interesting that the barks of piglets were generally ignored by adults, although juveniles sometimes responded with playful activity. However, the barks given by adults when alarmed usually resulted in alert stances and rapid locomotion in animals of all ages in the vicinity.

Many of the behaviour patterns listed as occurring in non-play rarely occurred in juxtaposition to play markers, and they tended to be high-priority patterns for young piglets. They included behaviour associated with obtaining milk, solid food, water, sleep and warmth, and avoiding injury from conspecifics. However, although occurring more frequently in non-play, sniffing the ground, rooting, shovelling and sniffing and biting objects often appeared

playful, in that they were performed in a rapid, jerky manner. Presumably they were not sufficiently associated with play markers to be included frequently in play bouts (as defined in this study).

The total frequency of the behaviour patterns performed in play varied between individuals and between groups. For example, comparing the behaviour of blw and yo between birth and the death of yo (who lost her teat when blw switched litters) showed that blw played significantly more than yo. Towards the end, yo spent most of her time lying on her belly in a hunched position in contact with others. A comparison of WB's three piglets showed changes in their relative levels of play during development. Between birth and eight days, wy played significantly more than bp and bo, while between nine and seventeen days she played more than bo and less than bp, and between eighteen and forty-one days she played less than bo who played less than bp. Comparing the levels of play shown by different groups of piglets, a group of six February born piglets weighing less than 40 kg at thirteen weeks of age played significantly more between six and thirteen weeks than a contemporary group of seven piglets weighing more than 45 kg. The focal piglets sampled from the August litters played significantly more than those born in February above six weeks of age, but before this results were variable between litters and across seasons. Bad weather during the Spring was probably the main factor affecting the level of play at this time, through its effect of lowering the overall activity of the piglets and forcing them to huddle together in the nests.

Sequences

In order to illustrate the arrangement of behaviour patterns in sequences, positively significant first-order transitions occurring in play are presented in Figures 1.35 and 1.36 for the periods one to eight days, and nine to seventeen days. (Although arranged in flow diagrams, transitions above the first order are not necessarily significant.) For comparison, lists of significant transitions occurring in non-play are presented in Appendix C. As play markers were relatively infrequent during the first seventeen days, play bouts were short and few transitions were significant. Between one and eight days, most behaviour was organized around resting and suckling while in the nest, and walking and exploring objects and other pigs while active. Between nine and seventeen days, frequent transitions between scampering, trotting, grunting, walking and standing occurred during play. In non-play, walking and sniffing the ground were the foci around which most other behaviour was centred.

As the behaviour patterns significantly associated with play remained the same over subsequent age periods, and as play seemed to take the same form, the remaining data (18-91 days) was lumped in order to produce higher numbers in the majority of boxes in the transition matrix. This meant that more transitions could be tested for significance by the chi-squared test, as their expected values were higher than five. Therefore, more significant transitions were obtained, giving a more comprehensive representation of the sequences of behaviour occurring during this period. The positively significant transitions involving play markers are shown in Figure 1.37, while the numerous others occurring in play and non-play

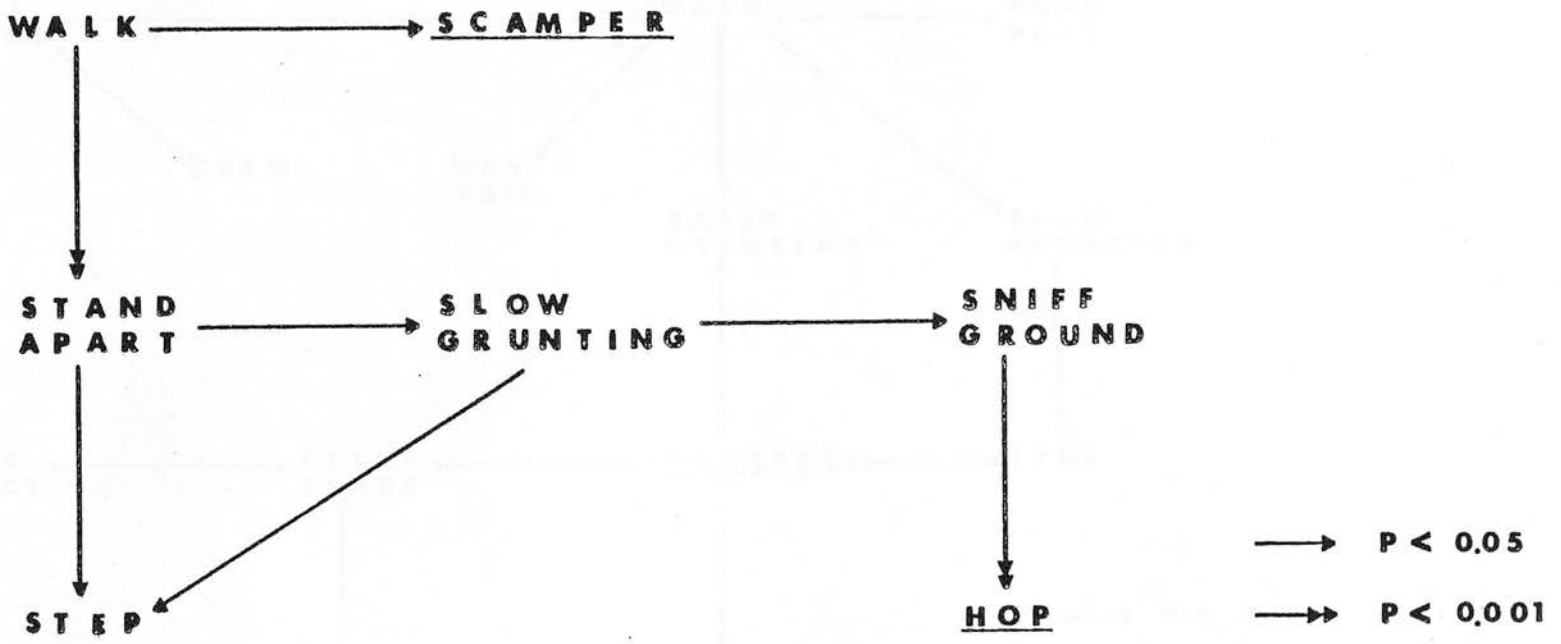

Figure 1.35 Significant transitions performed during play bouts in the Pig Park; 1-8 days (play markers underlined)

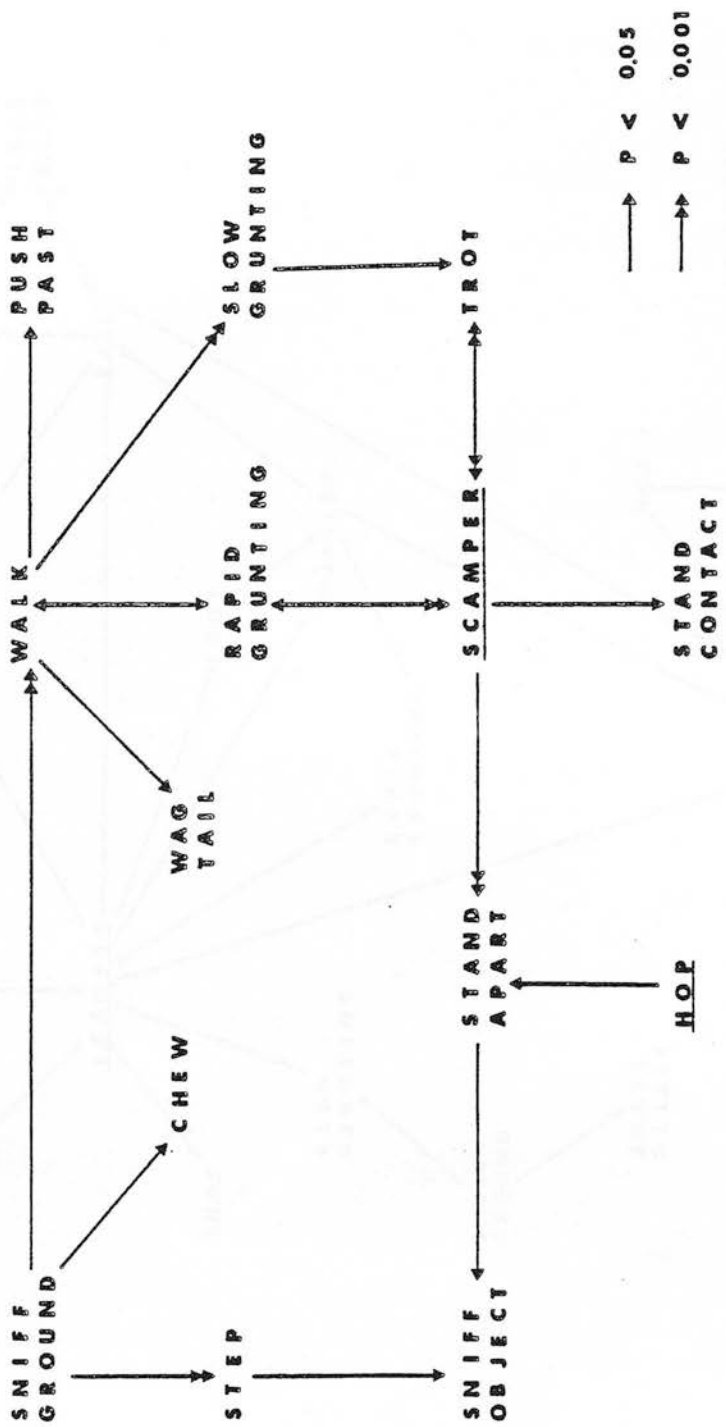

Figure 1.36 Significant transitions performed during play bouts in the Pig Park; 9-17 days (play markers underlined)

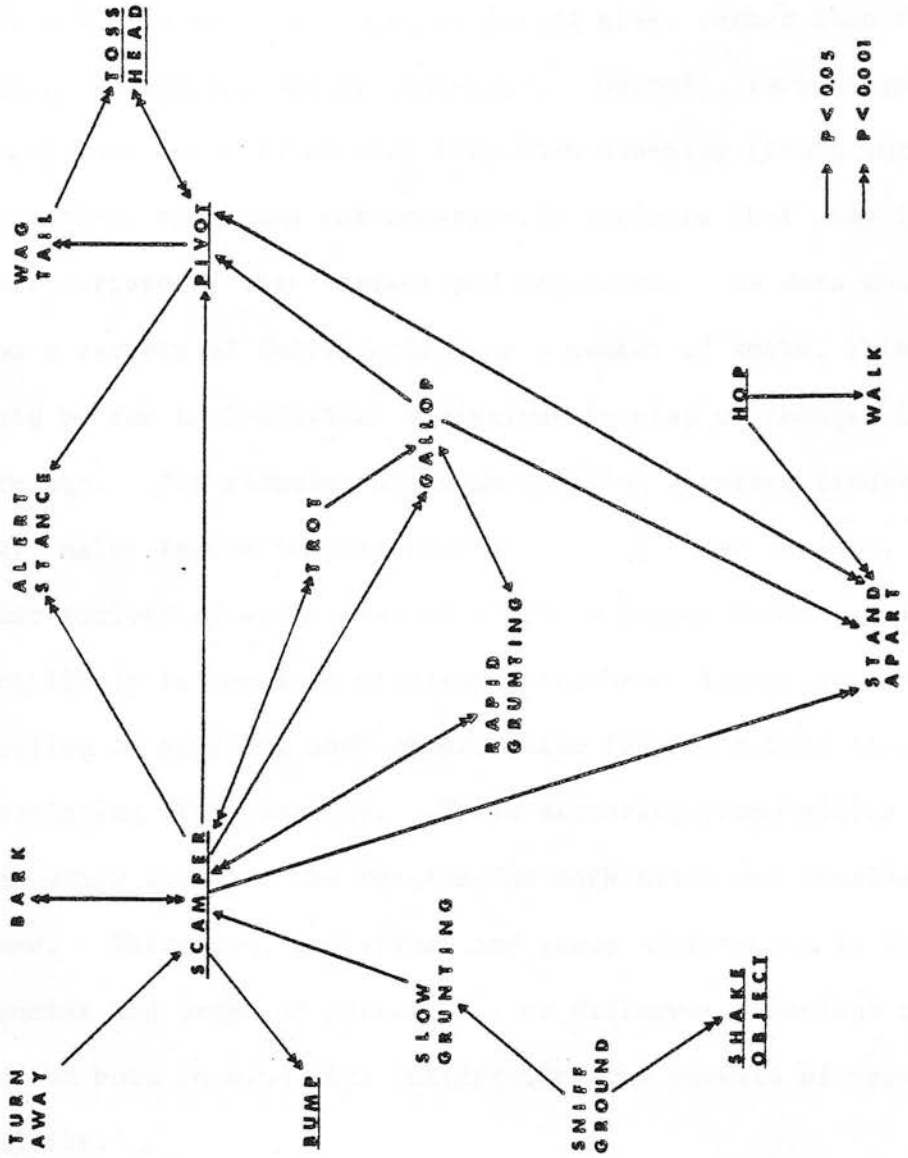

Figure 1.37 Significant transitions involving play markers (underlined); 18-91 days

bouts are listed in Appendix C. Many of the transitions significant in play were also significant in non-play, indicating that play and non-play overlap. Scampering was the most common play marker, and appeared frequently throughout play bouts, while other play markers occurred less regularly. Play markers were interspersed with other behavioural elements during play, rather than forming a closely integrated set of behaviour. Overall, fewer significant transitions occurred in play (75) than non-play (163), but although suggestive, this does not necessarily indicate that play involved a wider variety of less stereotyped sequences. As data was pooled from a variety of individuals over a number of weeks, this result could be due to individual variations in play or changes in play with age. For example, although circling occurred frequently in play, males tended to perform more circling than females, and in a wider variety of sequences, as shown in Figure 1.38. Males were more likely to continue circling after brief transitions to standing, kneeling or sniffing each other, while females tended to scamper in association with circling. These differing propensities cancel each other out when the results for both males and females are combined. Therefore, individual and group differences in the frequencies and order of performance of different behaviour patterns must be born in mind when interpreting the results of sequence analysis.

In order to determine whether rôle reversal occurred in piglets, the number of times which each member of WB's litter avoided each other member was compared for play bouts and non-play bouts. There was no significant difference between the two, suggesting that dominance relationships were upheld during play ($\chi^2 = 7.03$; d.f. = 3; $p > 0.05$).

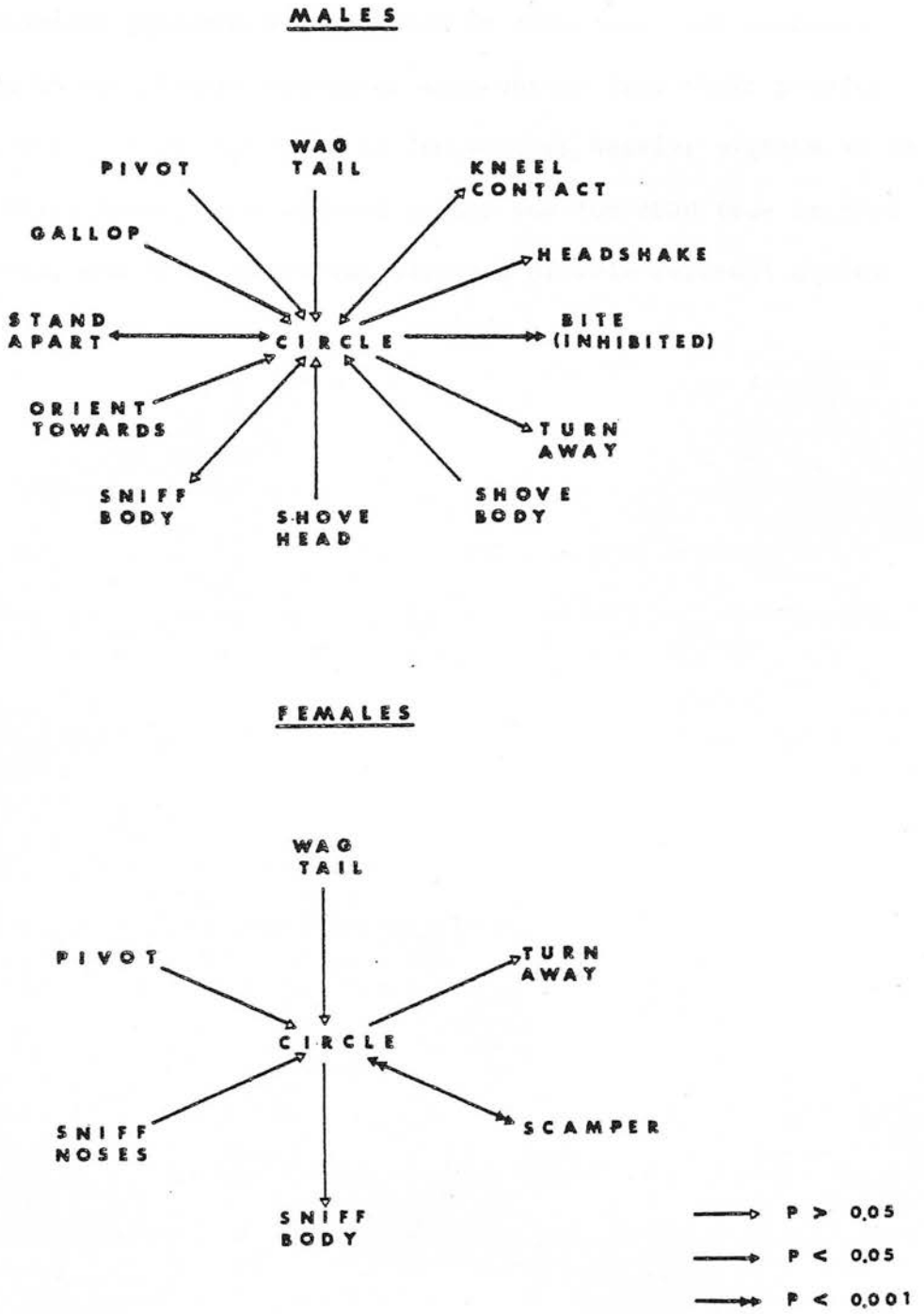

Figure 1.38 Transitions involving mutual circling which occurred more than four times during play bouts in the Pig Park; 18-91 days (Social behaviour patterns include both giving and receiving the behaviour)

To sum up, play in piglets did not form a unitary category of behaviour and was not necessarily more random than non-play. However, behaviour patterns were altered in form, and some elements occurring in non-playful sequences were absent from their playful counterparts. Play was not more frequent in heavier piglets or in piglets which seemed less reliant on the sow for food (see section on weaning), and no evidence was obtained of rôle reversal during play.

DISCUSSION

Suckling behaviour

The finding that sows tended to use characteristic positions for suckling is in keeping with the findings of Gill and Thomson (1956). As standing to suckle was limited by the ability of the piglets to reach and provide adequate stimulation of the udder, it did not become common until the piglets were at least three weeks old, and occurred mainly while away from the nest. If standing, rather than lying, is adaptive in permitting greater vigilance and quicker reaction to predators, the tendency of sows with young piglets to return to the nest before lying to suckle them may be related to their greater need to suckle in a secluded or defendable place.

The growth rates of piglets suckling from different teats did not indicate a consistent advantage in sucking the anterior or upper row teats. In studies in which a small advantage has been found, the results have been based on average findings from a large number of sows and litters (e.g. McBride *et al.*, 1965; Fraser and Morley-Jones, 1975). Even if some piglets do have lower yielding teats than others, they may be able to compensate by increased consumption of solid food. In fact, Barber *et al.* (1955) found that a close correlation between milk yield and weight gain over the first three weeks of age disappeared over the next five weeks as more creep food was eaten. In addition, effects of milk yield on growth in the Pig Park may have been confused by the propensity of opportunistic piglets to suckle from vacant teats on the udders of their own and other mothers as well as from their regular teat.

If one or two piglets continually obtained more milk than their littermates, this would only be an advantage to the fitness of the sow if they were much more likely to survive and reproduce. This is unlikely, because a long period elapses between birth and puberty, during which the risks of predation, crushing and starvation are present to all piglets. Therefore, one might expect early mortality of weak piglets, followed by adequate investment in all survivors, and this does appear to occur.

From observations in the Pig Park, it is suggested that a number of factors are involved in the initial selection of teats, including the number of piglets present at the udder, the ease of extraction of milk from individual teats and the amount obtained, attraction towards the anterior end of the udder due to the vocalizations of the sow, and the position of the sow at successive sucklings, including the side lain upon and the degree of udder rotation. Differences encountered at various positions along the udder may be affected by such individual attributes as relative size, vigour, aggressiveness, tendency towards a stereotyped preference for one teat, tendency to adapt to changing circumstances and teat searching strategies. The observations of McBride (1963), Hemsworth *et al.* (1976), Scheel *et al.*(1977) and Lien and Klopfer (1978) support these ideas.

When vigorous fights occur at the udder, one might expect that the winners would also be successful in winning fights with the same individuals away from the udder. However, as few observations were made of vigorous fights both at and away from the udder, and as the outcomes seemed to depend partly upon the relative motivation of the combatants to fight, it cannot be assumed that the winning of a teat

indicates a general ability to dominate others. As piglets at both ends of the udder tend to be involved in fewer fights over teats than those in the middle (Fraser, 1975b), and as these fights are unlikely to occur between every dyad in the litter, the concept of dominance when applied to the teat order seems unjustified.

It is interesting to speculate upon the switching of teats by blw and py. When py switched from 12's to 2's udder, she gained weight more rapidly than all but one of her former littermates (see Table 1.2). This suggests that her new teat was initially more productive than her previous one and/or that she was able to stimulate the ejection of more milk from the new teat. It seems likely that the new teat was preferred due to its greater accessibility, being at the end of the udder of a sow who stood to suckle rather than between the teats of others on the udder of a sow who lay to suckle.

In the case of blw, it is probable that the initial switch from RR's to 2's udder occurred when the two sows suckled in synchrony in the same nest. If blw's teat had not been accessible due to crowding in the nest, he may have jumped round, pushed in at 2's udder and obtained a milk let-down. The new teat was in a similar location to his previous teat, in keeping with the finding that a foster piglet in a foreign farrowing crate will usually attempt to suckle from the teat corresponding to the preferred teat on its own mother's udder (Horrell and Bennett, 1981). After the initial suckling, the quantity or quality of 2's milk may have attracted him to suckle from her. As she suckled less frequently than RR and 12, and as her piglets grew at a comparable rate, it is possible that she let down a greater volume of milk at each suckling than the

other sows. Although a less plausible explanation, it could be that blw was attracted to rb's teat because of some social interest in rb, or because previous social experience indicated that he would be able to compete successfully for rb's teat.

One might expect that in social environments in which unrelated young are present, one would get the evolution of mechanisms by which a mother could distinguish between her own and other young and feed only her own (Gubernick, 1981). Although there is no doubt that sows can distinguish between their own and unfamiliar young by olfactory means (Meese and Baldwin, 1975), it is not clear whether they can recognize individuals from their own and other familiar litters. Even if they could, there was no indication that the sows in the Pig Park knew precisely how many piglets they had or that they would wait until all piglets were present at the udder before suckling (as suggested by Lent, 1974). Aggression towards piglets was rare until weaning when it was directed indiscriminately towards all piglets in the close vicinity, and prior to weaning, no attempts were made by the sows to exclude particular piglets from suckling. Although a greater degree of familiarity existed between a sow and her own piglets, which probably enabled her to identify them, this did not prevent her from suckling the piglets of other sows.

The onus for locating and defending teats fell on the piglets themselves. That piglets approached their own mother from a distance and went straight to their teats indicates that they could identify her visually. They also responded to her grunts when she was out of sight by approaching her rather than other grunting sows. Once at the udder, they knocked at non-littermates which pushed in at the udder, and they defended their teats from all other piglets.

The existence of dominance relationships between at least some pairs of piglets suggests that individual recognition was possible, and so it seems likely that the piglets knew who belonged at the udder and who did not.

Once a stable teat order was formed, the suckling behaviour of the sow and her piglets is closely atuned, in that each piglet goes quickly to its own teat and stimulates milk let down rather than wasting time and energy competing for teats. The sow is then able to deliver a more or less equal amount of milk to each litter member quickly and efficiently. By providing milk only when sufficient stimulation of the udder has occurred, it is likely that all of the sow's piglets will be present. However, she cannot afford to be too responsive to the absence of some piglets from the udder or fighting over teats. All of her piglets would suffer if, for example, she refused to suckle them because one was missing and perhaps dead.

The suckling intervals in the Pig Park tended to be longer than in a modern farrowing house, possibly because piglets had more to occupy their interest, making them less likely to go to the udder at every disturbance. Also, the sows may have been less willing to suckle while occupied in the activities of foraging or social interaction, which are prevented in sows kept in farrowing crates. However, the percentage of sucklings which did not result in the let-down of milk was higher in the Pig Park, indicating that this was not a phenomenon exclusive to intensive housing systems. The probability of let-down was decreased when (a) only a short interval had elapsed since the previous successful suckling, (b) when the sow was disturbed by conspecifics (e.g. courting males, juveniles) and (c)

when the observer approached too closely. That piglets gained weight at a lower rate than those kept intensively was probably due partly to the greater energy expended in locomotion and keeping warm and partly to a lower milk yield from the sows. Barber *et al.* (1955) found that sows allowed to suckle their young at one hour intervals produced more milk than sows suckling at two hour intervals, and the low suckling frequency of the sows in the Pig Park may have also had this effect.

Sucklings were often synchronized and this reduced competition and interference from non-littermates over that occurring when a sow suckled in the absence of their mothers. As disruption due to competition with non-littermates can result in a reduction in the probability of milk ejection, which might decrease the weight gain of piglets if common (Horrell, 1982), synchronization of suckling could conceivably increase the inclusive fitness of a group of related sows. This might explain why a sow sometimes synchronized a suckling with another sow even though she had suckled recently and was unlikely to yield any milk. One might otherwise have expected her to refrain from suckling, thereby encouraging her piglets to seek extra milk from the other sow.

Communal suckling is reported to occur in wild and feral pigs (Kurz and Marchinton, 1972; Lent, 1974). In mice, Saylor and Salmon (1971) discovered that communal suckling from two mothers improved the weight gains of pups in both litters over those of pups reared by one female because the pups were able to suckle for longer periods. In lions, where female group members are closely related, communal suckling increased the survival rate of cubs over those suckled only by their own mother (Bertram, 1976). However,

observations in the Pig Park would suggest that piglets suckle from other sows in an opportunistic way, taking advantage of teats in the absence of their owners. True communal suckling, whereby piglets suckle indiscriminately from all sows, does not occur.

The finding that the sows farrowed in separate nests and only started resting and suckling together after one or two weeks, stresses the importance of the formation of a teat order within each litter. By farrowing alone, each sow ensures that she produces milk only in teats which are being used by her piglets. She also ensures that her piglets obtain colostrum from her on the day of birth, which might not happen if she was to farrow in the same nest as a sow with older piglets. Older piglets might then compete more effectively for her teats, causing her piglets to have difficulty in obtaining teats. Finally, by remaining apart during early life, piglets have the opportunity to learn the identity of their own mother and to approach her for milk.

The factors determining the precise age at which piglets are weaned from their mother's milk are hypothetical. Age at weaning did not appear to be determined by the amount of aggression received from the sow, as this varied between sows and could start a long or short time before the completion of weaning. The energy obtained from solid food and the energy expended in keeping warm may have had an effect, as, if piglets were obtaining more solid food and suckling less frequently, the milk supply might have dried up earlier. The nutritional state of the sow might have affected the timing of oestrous periods after farrowing, which may have had a small effect on the age of her piglets at weaning. Gill and Thomson (1956) found that a reduction in milk yield at six weeks coincided with

oestrus in the sows. The time of year appeared to have an effect, in that the February born litters were suckled for longer than the August born ones, regardless of their ages when their mothers became pregnant. A reduction in day length or food quality in the Autumn might have promoted the weaning process. It is also possible that the amount of udder stimulation received by the sow indicated the strength and vigour of her piglets. Once they became too rough, the sow might have avoided them, thus reducing the level of stimulation, which could lead to a reduction in milk production. This might further explain why the smaller Spring and Summer litters were suckled for longer than the large August litters.

The weight of individual piglets could not be used to predict their probability of missing sucklings or weaning themselves. However, there was a suggestion that the relative accessibility of teats and the ability of piglets to stimulate them and maintain a good supply of milk, did affect their propensity to look elsewhere for food. Piglets at crowded middle and lower teats were more likely to turn away from the udder immediately after let-down than to massage and hold their teat. Jeppesen (1980) found that intensively reared piglets which spent a longer time holding their teat after suckling had higher growth rates, suggesting that the duration of holding teats was a measure of their satiation. Therefore, piglets quick to move away from the udder may eat more solid food at an earlier age. However, more work is needed in order to elucidate the factors affecting age at weaning.

Resting behaviour

Maternal aggression during the first week after farrowing was

instrumental in preventing juveniles and adults from resting in the farrowing nest. When other animals did rest in a nest with neonates, the piglets were at risk of being crushed, and their resting and suckling bouts were disrupted. No studies have yet been made on the physiological control of maternal behaviour in sows (Rosenblatt and Siegel, 1981). In mice, stimulation of the nipples by the suckling actions of the pups is important in initiating maternal aggression (Svare, 1981) but in sows, the high level of oestrogen and low level of progesterone present in the blood just prior to farrowing (Ash and Heap, 1975) may be related to the onset of nest building and nest defence at this time. Nipple stimulation and prolactin may be involved in the maintenance of maternal aggression. The initially low level of maternal aggression shown by the gilt, WB may have been due to her lack of previous experience in rearing young. Juvenile females did not exhibit maternal behaviour, but this may be inconsequential, as there is no hard evidence that 'aunting' behaviour in primates improves their ability to care for their own young (Harper, 1981). The maternal aggressiveness of all domestic sows has probably been reduced to varying extents compared with that of wild sows, through artificial selection for sows with young piglets which remain calm in the presence of humans. In close confinement, aggressive sows might accidentally trample on their piglets in their attempts to defend them, as was reported by Hodgson (1935).

The distances between the farrowing nests of wild and feral pigs have not been reported, but in the Pig Park they varied considerably. Wild sows may co-operate to attack a predator when a piglet is seized (Frädich, 1974) but whether or not this occurs

during the early period of isolation in separate nests is not stated. Observations in the Pig Park suggest that maternally responsive sows will react to the distress calls of any young piglet, but the decision to approach the source of the call will depend upon whether or not the sow is in her nest with her piglets.

During the first few days *post partum*, the sow spends long periods in the nest, and this is important in maintaining the body temperature of her piglets. However, with the increasing nutritional demands of the piglets, the sow must spend increasing lengths of time foraging. In large litters and in warm environments, the piglets might be able to keep warm on their own by huddling together. On the other hand, small litters and cold climates may prompt the early merging of litters in a communal nest. As well as obtaining additional warmth by huddling with non-littermates in the absence of their mothers, the piglets might benefit from the warmth and protection of additional sows, visiting the nest at different times. It should be noted, however, that the sows did not take regular turns 'baby-sitting'.

A number of factors affected the timing of communal nesting as well as the identities of the animals resting with a new litter of piglets. The relative age of different litters played a part, in that older litters were likely to move into the nest of a younger litter. The relative quality of different nests was also important, in that juveniles were attracted to the farrowing nests, which tended to be more sheltered and drier than the simple hollows usually made by non-maternal animals. This was due to the nest building activity of the pre-parturient sow as well as the additional protection provided by humans, which would suggest that

the same attraction to farrowing nests might occur in the wild. Therefore, the declining level of maternal aggression and/or increased boldness of juveniles, particularly during inclement weather, probably determined when they first rested with the piglets. Finally, the social bonds of the mothers were important. Social bonds were strongest between highly familiar animals, especially between mother and daughter sows such as 2 and RR, and 4 and WB, which probably explains why these pairs were relatively quick to rest with each other after farrowing. Familiarity was also affected by the relative lengths of time which different individuals had been kept together in the same enclosure, which affected the nesting arrangements of the adults from the forest and gorse enclosure sub-groups. The juveniles preferred to rest with sows belonging to their own sub-group, although not necessarily with their own mother. As synchronized farrowing did not occur between all sows in the Pig Park in 1980, it is not known whether the presence of piglets would have drawn them together sooner after the merging of the two sub-groups. However, it is interesting that, whereas RR was first to enter her mother, 2's nest, later followed by her piglets, it was WB's piglets who first entered the nest of the unrelated sow 12, followed later by WB.

Once piglets had started to rest in different nests, they became more and more likely to rest with other animals. They seemed less tied by social conventions than their mothers, and would rest with any resting animals if their regular nest was empty. Presumably, as they grew older and were suckled less frequently, the need to remain with their mother while active, and in their own farrowing nest while resting, became lower. They might also have

been better able to predict when to approach their mother for milk and to locate her quickly when she started grunting. In addition, their increased awareness, co-ordination and speed was tied with a reduction in the maternal responsiveness of their mother. However, even after weaning, they were still more likely to rest with their mother and littermates than with other individuals, perhaps due to their greater familiarity. It is not known whether weaned littermates would continue to rest preferentially with each other, if kept in a group with familiar non-littermates in the absence of their mothers, but it is possible that the gender of individual littermates and non-littermates would become increasingly important in determining their resting preferences as well as their other social preferences.

Social facilitation

The analysis of inter-individual bouts of a number of behaviour patterns indicated that piglets were more likely to be included in the same bout with each other and their mothers than with other group members. Although the synchronized performance of rubbing and scratching on one occasion might be due to a common attack of biting flies, and the synchronization of drinking to common physiological requirements, it was unlikely that the same individuals would occur repeatedly in different bouts. Also, as the trees used for rubbing, streams for drinking, observer for nosing and unusual objects for nosing were available for much longer periods than the time spent in their use, the close synchronization of these four different types of activity on separate occasions by the members of particular sub-groups suggested the passage of social

influences between those animals. On the other hand, relatively high similarities between particular pairs of piglets were not found, implying that social facilitation was not based on the individual identities of the participants. It seems more likely that the performance of a distinctive activity by one animal attracted the attention of other animals in the area and increased their probability of performing the same activity. As piglets and their mothers were most often together, social facilitation between them was most common. Finally, as the first animal in a sequence varied considerably, there was no suggestion that particular animals were more effective in initiating inter-individual bouts.

Dominance relationships

The use of the concept of dominance implies that the dominant member of a pair has priority of access to important resources over the subordinate member. However, when piglets lost a fight, or avoided others, it was often not clear whether they were competing for a particular resource, or whether the outcome of a competition depended upon the relative motivation of each piglet for a resource. One may wonder why littermates fought away from the udder during their first two weeks, when the fights did not appear to be related to fights at the udder, and when their basic requirements for milk, warmth and protection were provided. However, dominance relationships tended to remain stable for long periods, and piglets successful in inducing avoidance by others were likely to benefit later on by obtaining priority to favoured items of food. In intensively reared pigs, McBride *et al.* (1964) found that social rank was positively correlated with weight at eight weeks, and high ranking pigs

gained weight more rapidly than low ranking pigs over the next two months. However, Meese and Ewbank (1972) discovered that previous experience in being high or low ranking did not prevent strangers from establishing new dominance relationships based on current fighting ability, which was presumably determined by factors such as aggressiveness, strength and agility.

If, in the wild, daughters remain in their mother's social group after puberty, dominance relationships established early in life with other female group members could have long-term consequences on their reproductive success, as younger females would remain subordinate to older ones.

Dominance relationships formed between peers would probably be more susceptible to change. It is unlikely that early dominance relationships formed between male peers would affect their mating success several years later when able to compete effectively with older males for oestrous females. By this time it is likely that they would be relatively solitary and using different home ranges, so that they might not be familiar enough to recognize a previous dominance relationship when meeting in the presence of oestrous females. In support of this idea, Ewbank and Meese (1971), found that after periods of separation from an established group of over twenty-five days, fighting was more common when the isolated pig was returned to its group than after shorter periods of separation. Also, the social rank of the isolated pig was more likely to change upon re-introduction to its group. Therefore, although early dominance relationships between male piglets might affect their survival to reproductive age, through their effect on priority of access to food, it is unlikely that they would be of importance

during competition for oestrous females.

As dominance relationships did not prevent piglets from making frequent contact with one another, it is apparent that they were not the sole factors affecting the social behaviour of piglets. Although more clear dominance relationships may have been obtained by observing competition over creep food, it is important to remember that a high ranking animal at the feeding site was not necessarily avoided away from the feeding site, and sometimes avoided others when, for example, its current motivation to interact and play with others was lower than its motivation to suckle, rest or eliminate. These changes in the probability of avoidance probably explain why clear dominance relationships were not obtained between all group members in this study. In addition, the relative distances over which the opposing forces of avoidance and attraction operated between members of different age-classes and different litters no doubt affected the probability of recording avoidances within particular dyads.

Nearest neighbours

Although the measurement of nearest neighbours showed up clear differences in the probability of being nearest to littermates, non-littermates, the mother, other adults and juveniles, it did not reveal obvious preferences among piglets for particular social companions. This would make sense if a piglet's survival depended upon the presence of a number of other piglets around it, regardless of their identity. By keeping together, the combined senses of the group might speed the awareness of dangerous situations and/or decrease the time spent in vigilance over that of a solitary piglet.

Since piglets do not run to their mother for protection when alarmed, but run together under bushes, group membership might decrease an individual's own chance of being caught by a predator. It might also enable the mothers of young piglets to locate and defend them more easily than if they were all spread out.

If remaining in a close group is important to a piglet's survival, it would not be an advantage for it to synchronize its movements with one particular piglet over all others, because that piglet could die or disappear, leaving the other without a social companion. By associating with all piglets, it can remain well-integrated with them and freely join any sub-group of familiar piglets whether they are active or resting in a nest.

Measurements of changes in the time spent at various distances from the mother and the frequencies with which a mother and her young move towards and away from each other have been used to describe changing mother-infant relationships in primates (Hinde *et al.*, 1964; Owens, 1972) and New Forest ponies (Tyler, 1972). This approach was not practical in pigs because the mother was not the only base from which the piglets made movements into the surrounding environment. Young piglets ventured short distances from their nest site and returned to it both in the presence and absence of their mother. They also moved further distances away from their nest with their mother, and then remained in a huddle under bushes while she fed. This huddling site could then be used as a base for short forays, or the whole litter could move to a new site or return to their nest. Although their mother controlled their movements to some extent by calling them to her, she did not actively restrict their movements, as might a primate mother (e.g. Altmann, 1980).

In addition, whereas in primates, the infant gradually attains independence over a number of months, in pigs the period in which the mother frequently takes an active rôle in making contact with her piglets is confined to the first two weeks, after which the piglets are mainly responsible for initiating contact, usually in the context of suckling.

The use of nearest neighbour data showed up the basic social relationships of piglets quite well. However, as piglets often associated in close sub-groups, a more detailed analysis of the relative orientations of sub-group members might have revealed more subtle social relationships between individuals. Lazar (1974) has used this approach in ferrets, *Mustela putorius*, in a study of social play between littermates, and Emory (1976) used orientation between members of captive groups of mandrills, *Mandrillus sphinx*, and geladas, *Theropithecus gelada*, to examine attention structure within the groups.

It might also have been interesting to measure social development by determining distances between piglets and individuals of different ages, sexes and degrees of relatedness at increasing ages. However, it is likely that these distances would have varied widely depending upon the activity of each animal, their previous activities, climatic conditions, the reproductive state of their mothers, the distribution of resources, the presence of predators or other alarming stimuli and the availability of individuals within each category.

Social interactions

A number of factors affected the probability that overt social

interactions would occur between particular individuals. Firstly, the availability of different categories of pig affected the social development of litters born at different times during 1980. The February born litters varied in size, which might have affected the early behaviour of the piglets, but once the piglets started to associate with non-littermates, they had a large choice of piglets with whom to interact. The August born piglets had an even larger choice of both littermates and non-littermates. However, WB's June litter was small, and born at a time when other litters of similarly-aged piglets were not available. WB's piglets interacted much more with each individual littermate than members of the other litters, which interacted more overall, but to a lesser extent, with each individual piglet. It is possible that, in the wild, piglets from small litters born out of synchrony with other litters would tend to stay together with each other and their mother for longer after weaning due to their relatively strong social relationships. Apart from litter size and relative time of birth, mortality and removal of juveniles from the Pig Park affected the availability of different categories of pig. Thus, the removal of juveniles at the beginning of April, resulted in an increased frequency of interactions between adults and the February born piglets.

Other factors affecting the early social experiences of the piglets included the relative aggressiveness of their mothers, which affected the probability of early social interactions with juveniles. (Such interactions were probably not beneficial to piglets in that they tended to receive rough treatment from the juveniles.) The social relationships of the sow affected the probability of meeting particular individuals while in the company of the sow, and

climatic conditions were important, as the piglets born in the Summer, when the weather was relatively warm and dry, were more active and interacted more frequently with each other than the piglets born in February. Also, the tendency of group members to crowd together in one nest during bad weather, when other nests were flooded, increased the frequency of aggressive knocks occurring between individuals which did not usually rest together. Attributes of the piglets themselves, such as their relative health, vigour and aggressiveness, and their increasing familiarity with their social and physical environment affected the form, direction and frequency of their social interactions, and finally, the attractiveness of the piglets to other individuals influenced their probability of interaction with piglets.

Although different litters and different individuals had varying social experiences, it is not implied that these differences necessarily resulted in long-lasting differences in their social behaviour. As Bateson (1976) points out, internal regulating mechanisms may act to buffer the effects of external forces, making it difficult to distinguish between adults with different histories. Although much attention has been paid to the effects of early experience on future behaviour (e.g. Clarke *et al.*, 1951; Harlow and Harlow, 1969; Immelmann and Suomi, 1981), it is important to distinguish between the effects of early versus prior experience, and to consider the length and pattern of exposure to a particular environmental feature (Simmel and Baker, 1980). This type of detailed analysis was not attempted. However, hopefully the description of the range of behaviour occurring in a free-ranging group, and the factors affecting it under natural conditions, will provide a useful basis for future studies along these lines.

The finding that piglets were more likely to interact with their mother and littermates than with other members of the pig group cannot be used as evidence that the other animals were of no importance to the development of the piglets. It may be that the frequencies of certain types of interaction are not important provided that they remain above a certain threshold (e.g. necessary to maintain group membership, lactation, etc.). Also, the presence of a particular class of individuals may have important effects even in the absence of overt social interactions. For example, the pheromones received from an adult boar by pre-pubertal females are known to lower the age at which puberty is attained, and females reared from one month in the absence of an adult boar are less likely to stand for the boar or to show overt signs of oestrus than females reared in physical contact with boars, or within three metres of them (Hemsworth, 1982). Similarly, the rearing of males in groups with peers of either sex improves their sexual motivation over that of males reared in physical and visual isolation of other pigs (Hemsworth *et al.*, 1977). Work on feral pigs is needed in order to determine the amount and timing of contact of piglets with boars and other individuals under more natural conditions, as this may provide a clue as to when their presence may be most important.

The finding that the behaviour of sniffing noses while vocalizing was directed by piglets towards other adults and juveniles as well as their mothers suggested that it allowed for recognition of group membership and possibly increased the tolerance of older pigs towards younger ones. This shows the value of observations made in a rich social environment, as Whatson and Bertram (1983), studying individual sow-litter groups, thought that its most

likely function was to re-establish the identity of the piglets nursed by the sow, who would show aggression towards the piglets of other sows. In the Pig Park, it was the piglets who were responsible for determining who suckled from a particular sow.

Piglets did not show a great preference for interacting with piglets of their own versus the opposite sex, but casual observation of juveniles suggested that males circled and mounted more frequently with each other than with females at this time. In weaned elephant seal pups, *Mirounga angustirotris*, wrestling occurs almost exclusively between males (Rasa, 1971), and juvenile male squirrel monkeys, *Saimuri scuireus*, perform rough and tumble play and mounting at a higher frequency and to a greater age than females (Baldwin, 1969). Therefore, investigation into differences in the social interactions of male and female juvenile pigs should yield interesting results. Also, although in pigs the hormonal status of males and females differs throughout life, different androgens and oestrogens reach peak concentrations at different ages (Booth, 1982; Colenbrander *et al.*, 1982; Elsaesser, 1982), and work has yet to be done on their effects on behaviour between birth and puberty.

Play behaviour

As Bateson (1981) found in cats, *Felis domestica*, play in piglets did not form a unitary category of behaviour controlled by one motivational system. If it had, one would have expected that all play markers would have reached their peak frequencies at the same age and that they would have usually occurred together in play bouts. 'Shaking objects' seemed to be least closely associated with other play markers, and was probably controlled by a different,

but overlapping, mechanism. Also, other behaviour patterns which sometimes appeared playful but did not necessarily occur in bouts with play markers, may be controlled by separate mechanisms (e.g. rooting in a jerky manner, circling).

Using a large ethogram, sequence analysis showed that the behaviour of piglets was highly variable and did not consist of long stereotyped sequences of behaviour. As many behaviour patterns occurred in transitions with a wide variety of different behaviour patterns, it was not possible to say that behaviour patterns were re-ordered in play as opposed to non-play, or that they were fragmented or repeated more than normal. Nor was it possible to say that behaviour from different motivational contexts occurred in quick succession in play, because most behaviour patterns occurred in different motivational contexts in non-play as well, and the motivation of the piglet was not always apparent. However, it was true that some behaviour patterns were absent or altered in form in play versus non-play. For example, fierce fighting included biting and chasing whereas playful circling sometimes included inhibited biting and lacked chasing with biting. If it had been possible to distinguish consistently between playful and serious circling, or between inhibited and hard bites, they would have been recorded as separate behaviour patterns, and the behaviour associated with each could have been compared. However, they appeared to form a continuum of intensity. The best method of distinguishing between play-fights and real fights would probably be to consider a fight as playful only if it occurred between individuals known to be well familiar.

Mounting behaviour in young animals has been considered to be a

form of play by various authors (e.g. Steiner, 1971; Owens, 1972) because it occurs in the absence of other elements associated with mating in adults, and is apparently goal-less. However, if all piglet behaviour was compared with similar behaviour in adults, much of the behaviour of piglets would be considered playful because it did not serve the goals of adults. As piglets are adapted to their environment throughout development, and have goals which may differ from those of adults, it seems more reasonable to distinguish their playful behaviour from their own more serious behaviour rather than comparing playful young behaviour with serious adult behaviour. Mounting was rare in most piglets, and was not often associated with play markers. Nor was it emulative, encouraging others to play. Therefore, if it is to be considered as a play behaviour in piglets, it should not be lumped with other forms of play, but could be classed, for example, as sexual play.

If it is assumed that the behaviour patterns performed in play were synonymous with those of similar appearance occurring in non-play, then the play markers could be considered as altered forms of non-playful patterns. The word 'exaggerated' is not used as it implies that the amplitude of the movements or the speed of performance is increased, which is not necessarily the case. For example, if scampering is considered to be a playful form of galloping, then it is altered in that movements in the vertical plane are increased whereas speed is reduced. However, these two categories should probably have been lumped, as they formed a continuum, which allowed for inconsistency of recording. It was hoped to distinguish playful locomotion from serious running created by fear, but where the latter was indicated, it often graded rapidly into play and

vice versa, so that it was incorporated into play bouts as defined in this study.

Although adults rarely, and juveniles sometimes, scampered with piglets, they did not handicap themselves to the extent of circling with piglets. Their social play was too rough for the piglets, who avoided them and played among themselves. Even between piglets there was no evidence of rôle reversal, in that although either member of a pair could initiate an interaction, the same (subordinate) member was likely to terminate the interaction by moving away in both playful and non-playful contexts. However, the fact that piglets did not threaten or attempt to injure each other during social play would suggest that self-handicapping did occur.

It has been suggested by Loizos (1966) that play occurs in the absence of serious goals, when the primary needs of the animal have been taken care of. Although play, and general activity, were depressed in starving, sick and injured piglets, and during severe storms, play occurred under a wide range of conditions, and was stimulated by sudden stimulus changes, novelty, and even frustration when the sow refused to suckle a piglet. Therefore, except under extreme conditions, the level of play would not appear to be a good index of welfare in piglets.

It cannot be said that play has no function because its goals differ from those of adults. The most frequent playful activity of piglets was scampering, which occurred in association with other forms of locomotion, rapid changes of direction and alert stances. It is suggested that these behaviour patterns are important in promoting physical development. However, as well as long-term effects on future fitness (Fagen, 1976), this has immediate consequences, in

that by obtaining maximum speed, suppleness, strength and endurance, the piglet should improve its ability to escape from predators and other dangerous features of the environment (e.g. adults about to lie down, attacking conspecifics, etc.). As young piglets are more susceptible to such dangers than larger pigs, one would expect the evolution of adaptive behavioural and physiological responses enhancing their ability to escape, and locomotory play may be important in this respect. Of course, there is likely to be a limit to the amount of play which is beneficial to a piglet at a particular age, as, if too much energy is expended in play, the piglet could weaken, and require more food from the sow than she is able to supply. However, within the ranges observed in the Pig Park, there was no evidence that sows actively promoted or interfered with the play of their offspring.

As the performance of play behaviour by one piglet often induced others to play, it is likely that the rapid, eye-catching movements and alertness of playful piglets acted as play signals. Play markers contained these characteristics, as did other behaviour such as the rubbing of the body up and down against trees. There was no, one, highly distinctive movement or position which was used only at the beginning of a play bout in order to initiate play. It is suggested that the initiation and maintenance of play within a group of piglets by the use of rapid movements and vocalizations was important in keeping the piglets together. As the piglets did not form specific partnerships with particular piglets, but were attracted to groups of piglets, it is likely that group membership is important for survival to a reproductive age. If exercise is important to piglets, then one would expect them to play together as

a group. Thus, whereas the movements of an individual playing on its own might attract the attention of a predator to that individual, it could decrease its chances of being caught by playing with a group of other potential victims (Dawkins, 1976). By performing locomotory play alone, a piglet could also become temporarily separated from the main social group, which could result in its missing a suckling, drawing the attention of predators by its loud contact-seeking vocalizations and decreasing the ability of its mother and other adults to protect it from predators. When a number of piglets, especially littermates, scamper together, these problems are eliminated.

Whether or not the social interactions of piglets, such as circling and mounting, are considered as forms of play, they are not necessarily important in providing practice for their performance as adults, since they occur in the absence of other elements of fighting and mating behaviour. Also, Hemsworth *et al.* (1977) report that the mating dexterity of males was not affected by rearing them in isolation from three weeks to seven months of age. As mounting was rare in piglets in the Pig Park, it is probably not of great significance to their survival, although it may in some cases help to maintain dominance over other individuals, which could provide an advantage during competition for food. Play fighting may be of significance in improving strength, particularly of the neck and shoulder muscles, and may also be used in maintaining dominance relationships. There are many other potential advantages to be gained from social interactions, such as in learning how to behave appropriately to information received from others, but their importance in shaping the evolution of social play in piglets is not

known.

Concerning the definitions of play in piglets, the use of play markers was limited due to difficulty in distinguishing between playful and non-playful forms of the same behaviour. Therefore, behaviour patterns such as 'wagging the tail', which were obviously playful in many cases, but also occurred in other contexts, could not be used as play markers. It is concluded that the term 'play' is probably best applied to circumstances in which the performance of certain behaviour patterns attracts the attention of other piglets and rapidly induces them to participate in the same activities. Behaviour occurring in the contexts of suckling, ingestion of solid food, resting and escape from an obviously dangerous or unpleasant situation should be excluded from play, and play should be divided into different categories according to the type of behaviour occurring (e.g. play fighting, sexual play, object play, locomotory play). A single play marker typifying each category could be used to identify bouts of each type.

SUMMARY

Concerning suckling behaviour, piglet growth rates were not consistently influenced by the position of their teat, and the concept of dominance at the udder was not justified. Crowding at the udder was probably an important factor prompting piglets to seek milk (and solid food) elsewhere, but they did not exhibit true communal suckling. Piglets were mainly responsible for locating and defending their own teat from others. Synchronization of suckling was common, but suckling bouts did not always result in milk let-down.

During the first week of life, the piglets remained in and around their farrowing nest, which was defended from conspecifics by the sow. After this, they rested increasingly with other group members in communal nests. The social bonds of the sow, relative ages of different litters, climatic factors and relative familiarity with different group members, affected the resting associations of piglets.

Social facilitation of different activities occurred between animals in the same area and did not depend upon the individual identities of the participants.

Dominance relationships were formed during encounters early in life, and appeared to remain fairly stable throughout and beyond lactation. They were probably not of great importance prior to weaning.

The probability of social interactions occurring between particular individuals was affected by the absolute availability of different classes of pig and by the probability of different

individuals being found near to one another. This was influenced by the social bonds of the sow, her sexual cycles and her aggressiveness, as well as by the physiological requirements of the piglets.

Play in piglets fitted some, but not all, of the general definitions of play put forward in the introduction.

PART 2 - THE INCUBATORS AND FLAT-DECK CAGES

INTRODUCTION

The early-weaning unit at the Rowett Institute is being used to determine the feasibility of rearing piglets artificially, as this presents a number of theoretical advantages to the pig producer (Fowler and Varley, 1980). In the majority of conventional pig units, ten to fifteen per cent of live born piglets die before weaning (English, 1982), and a large proportion of these deaths result from crushing by the sow and starvation due to inability to compete for a teat. These factors are eliminated when the piglet is removed from the sow. It may also be possible to reduce the inter-birth interval of the sow, thereby maximising the number of litters born per year, by inducing oestrus and serving the sow soon after farrowing, rather than following the conventional practice of waiting until the piglets are weaned at three to six weeks of age before introducing the sow to the boar.

A major problem encountered when piglets are weaned at a very young age comes from their lack of resistance to disease, especially from *Escherichia coli*, which can produce harmful toxins and cause scours (Jeppesen, 1980). Piglets initially gain passive immunity from colostrum, which is continually available from the sow for the first eight hours after birth (Gill and Thomson, 1956). This passive immunity decreases over the next ten days, when the piglet's own immune system becomes active (Wilson, 1974). Survival is improved if piglets are allowed to suckle to obtain colostrum for the first twelve hours after birth before separation from their mother (Lecce, 1971), and in this investigation they remained with

their mother for approximately twenty-four hours.

Although some success has been achieved in the artificial rearing of piglets weaned at one day of age, it is necessary to ask how the behaviour of these piglets might be affected. The incubators provide a very barren environment for the young pigs, as a result of social isolation and physical restriction. One would expect that the rearing of piglets in incubators would have a dramatic effect on their behaviour due to the absence of their mother - their main provider of nourishment, antibody protection, warmth and defence, and other social companions with whom they associate during development. It was hypothesized that the piglets would develop abnormal behaviour in the incubators, which would persist after transfer to the flat-deck cages. Abnormal behaviour was considered to be 'that behaviour which does not correspond to, or is without object, which appears with sharply increased or decreased frequency, or which is abnormal in its motor pattern' (Sambraus, 1981) by comparison with that occurring in the rich environment of the Pig Park. Support for this idea comes from the work of Harlow and Harlow (1969), who reared rhesus monkeys in isolation. The monkeys developed various abnormal behaviour patterns such as self-clutching and stereotyped rocking. Later they exhibited abnormal social behaviour, including an inability to inhibit aggression, avoidance of physical contact, inadequate social play, inadequate sexual behaviour, and brutality and/or indifference to their offspring.

The development of abnormal behaviour patterns has important implications for animal welfare, as it may indicate that the animals are suffering under the conditions in which they are being kept. Factors which may affect production are also important. It may be

that early social isolation results in significant deficits in mating behaviour, as found by Hemsworth *et al.* (1977) in boars isolated at a later age, and it may result in increased aggression (Fox and Clarke, 1971; Archer, 1976). Therefore, this study looked at the immediate and more prolonged effects of artificial rearing on behaviour, from both a production and a welfare point of view.

METHODS

The piglets were born in farrowing crates, and remained with their mothers for their first twenty-four hours before being washed with disinfectant and passed through a hatch into the rearing rooms. Here they were placed in incubators, which were blue plastic Addis Bigger Bins, with perspex glass windows at the front and back, and epoxy-coated slatted metal floors. Two vents in the roof of each incubator allowed the circulation of 33°C air, which was filtered to exclude bacteria. Figure 2.1 gives the dimensions and lay-out of an incubator.

The piglets were fed on tinned Carnation milk, supplied automatically through a system of tubes to nipple drinkers, at hourly intervals. This feeding system was washed out daily with Savlon disinfectant and water. A plastic trough under the nipple drinker, which caught some of the milk spilled by the piglets, was also used for feeding solid milk pellets to the piglets twice daily on their last three days in the incubators. At this time they received water, rather than milk, at hourly intervals from the nipple drinkers.

Behavioural observations were made using two methods. Scan samples were made of the instantaneous behaviour of each of forty-eight piglets, at ten minute intervals over periods of at least one hour, distributed equally throughout the day between 0900 hours and 1700 hours. Thirty minute focal animal samples were also made. Twelve piglets were observed upon introduction to the incubators, and observations were continued on eight of these piglets, with the aim of following their behavioural development throughout the study.

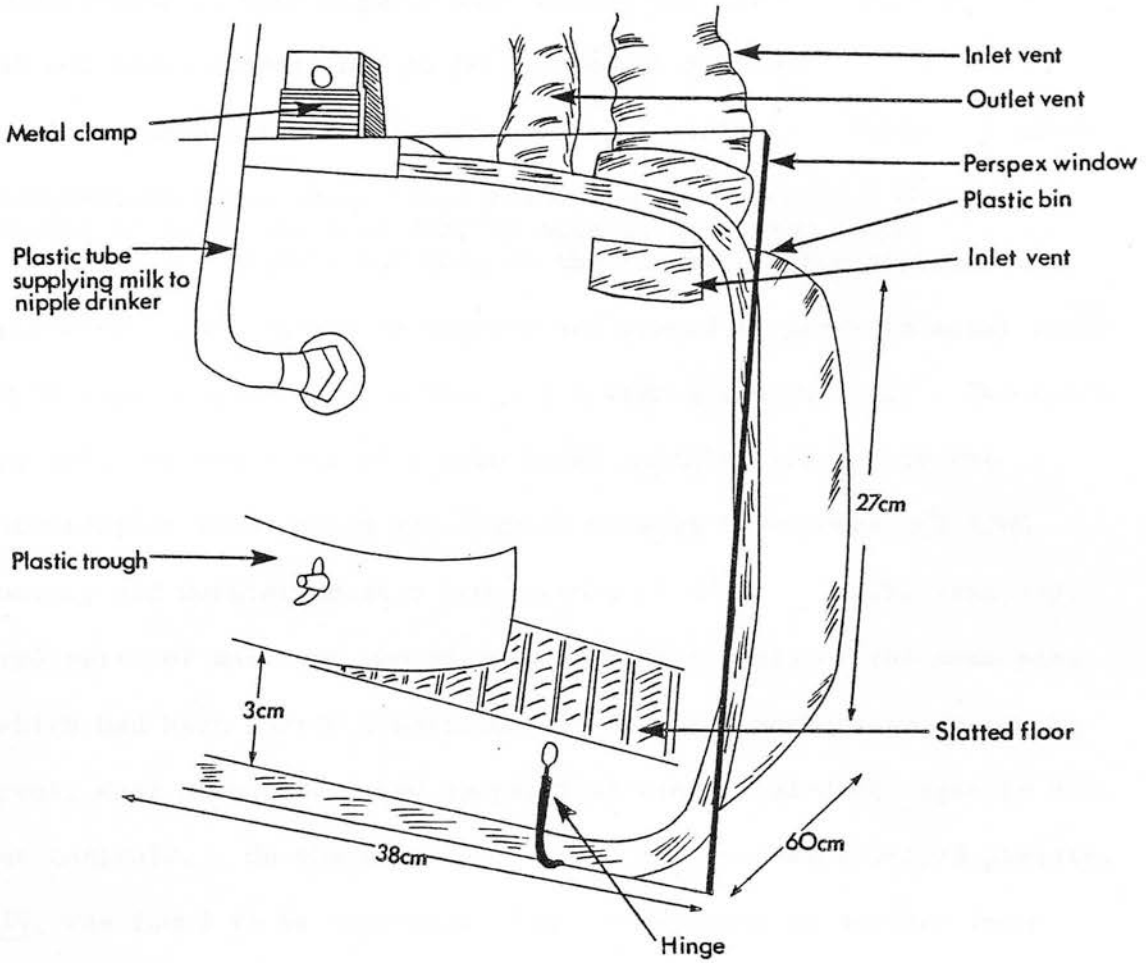

Figure 2.1 Drawing of an incubator

Unfortunately, many piglets died during the first week, and sampling of new focal animals had to be started as previous ones died, in order to maintain a sample size of eight piglets. Table 2.1 gives information about these focal animals while Appendix F shows the number of focal and scan samples made at different ages.

When the piglets had been in the incubators for approximately seventeen days, they were removed and placed in pairs in metal flat-deck cages measuring 1 m long x 1 m wide x 130 cm high. Two pairs of male and two pairs of female focal animals were put in the observation room, which was lighted between 0900 hours and 1700 hours, and maintained at a temperature of 25°C. On the same day, two pairs of male and two pairs of female piglets of the same age, which had been reared conventionally by their mothers in farrowing pens, were also introduced as pairs to other flat-deck cages to act as controls. On the next day, one of the incubator reared piglets, I9, was found to be very weak, and was replaced by another incubator-reared piglet, I22.

The piglets were fed twice daily (at around 0900 hours and 1600 hours) on milk pellets for twenty days, after which the food was changed to standard creep pellets. Water was available *ad libitum* from nipple drinkers.

On the day of introduction to the flat-decks, a forty minute video film was made of the behaviour of each pair of piglets. Thereafter, thirty minute tape-recorded focal animal samples, and ten minute scan samples, were obtained of the behaviour of each piglet until it was six weeks old (see Appendix F). Table 2.2 provides information about the focal piglets in the flat-decks. Observations were equally distributed between 0900 hours and 1700 hours.

The ethograms used for scoring the behaviour of the piglets in

Table 2.1 Focal piglets observed in the incubators

Piglet	Sex (Male = M Female = F)	Litter	Age at death in incubators (days)	Number of focal samples	Weight (kg)		
					Birth	1 week	2 weeks
I1	M	1	6	4	1.13	-	-
I2	M	1	5	4	1.10	-	-
I3	M	1	5	3	1.01	-	-
I4	M	1	5	3	1.34	-	-
I5	M	1	7	4	1.32	-	-
I6	F	1	6	4	1.10	-	-
I7	F	1	7	4	1.44	-	-
I8	F	1	-	12	1.05	1.56	2.84
I9	F	1	-	8	1.17	1.53	2.22
I10	M	2	7	2	1.65	-	-
I11	F	2	7	2	1.62	-	-
I12	F	2	7	2	1.75	-	-
I13	F	2	7	2	1.44	-	-
I14	F	2	6	1	1.42	-	-
I15	F	3	10	1	1.54	1.71	-
I16	F	3	-	6	1.34	1.65	2.65
I17	F	3	-	7	1.20	1.80	2.62
I18	M	4	-	7	1.15	2.76	4.28
I19	M	4	-	7	1.40	2.54	3.88
I20	M	4	-	7	1.33	2.56	4.28
I21	M	4	-	7	1.50	2.79	3.98

Table 2.2 Focal piglets observed in the flat-deck cages

	Cage number	Piglet	Sex (M or F)	Litter	Age at introduction of flat-deck cages (days)	Age at death in flat-deck cages (days)	Number of focal samples	Weight (kg) 3 weeks	Weight (kg) 6 weeks
Incubator reared	1	I18	M	4	17	-	9	5.00	9.1
		I19	M	4	17	-	9	4.10	9.3
	2	I16	F	3	18	22	2	2.50	-
		I17	F	3	18	28	3	3.60	-
	3	I9	F	1	17	-	2	2.40	4.9
		I8	F	1	17	-	9	3.20	8.2
		I22	F	4	17	37	7	4.40	-
	4	I20	M	4	17	-	9	4.90	7.6
		I21	M	4	17	-	9	4.50	9.0
Sow reared	5	S1	M	5	20	-	8	4.10	10.0
		S2	M	6	18	-	8	5.20	11.6
	6	S3	M	6	18	-	8	4.70	11.4
		S4	M	6	18	-	8	5.85	12.1
	7	S5	F	5	20	-	8	4.25	9.0
		S6	F	5	20	-	8	4.40	9.1
	8	S7	F	7	19	-	8	2.60	6.6
		S8	F	6	18	-	8	2.60	5.1

the incubators and flat-deck cages were basically the same as that for the Pig Park, with the obvious exceptions that behaviour patterns requiring the presence of another pig (social behaviour) could not occur in the incubators, while those necessitating a sow's presence (suckling behaviour) were impossible in the flat-deck cages. Alterations were made in the section on investigative and feeding behaviour to accommodate differences in the environments, and these are shown in Appendix D. The behavioural categories scored during scan samples are listed in Appendix F.

Analysis of frequencies, sequences and play bouts was performed using the methods described in Part 1 for the Pig Park data. The number of times each behaviour pattern occurred in the incubators, flat-deck cages and Pig Park was compared using the chi-squared test after calculation of expected values to allow for different lengths of observation time. First-order transitions occurring significantly more often than expected on the basis of a random model in the incubators and flat-deck cages were compared with those occurring in the Pig Park at the same age. Comparisons of the ratios of the twenty-three activities recorded during scan sampling at different ages and in differently reared groups were made by the 2 x 2 chi-squared test with one degree of freedom.

RESULTS

1 Introduction to the incubators

The behaviour of twelve piglets, I1 to I7 and I10 to I14, was observed upon introduction to the incubators. These piglets, from two litters, had been resting in huddles by their mothers before transfer. Upon introduction, they all stood tensely, listening, and stepped about in the incubators in a wobbly manner. They seemed to have difficulty walking on the slatted floor, which was slightly bouncy and was sloping towards the back. Eight of the piglets performed very little investigation or vocalization, but lay down by the wall to rest within three minutes of introduction. However, piglets I6, I7, I10 and I14 became agitated, stepping back and forth across the front window, prodding their noses at the window and grunting and squeaking frequently. They appeared to be trying to escape. They were active for between forty and sixty minutes before lying down for a long rest (i.e. longer than three minutes), but such long periods of activity are unusual for day old piglets. When they first lay down, all of the piglets shivered while lying listening in a tense, crouched position with the belly raised off the floor. Several piglets got up and lay down a number of times before settling down and closing their eyes. It is likely that the piglets had been chilled during washing and transfer to the incubators, and that the incubator floors were uncomfortable to lie on, and it is also possible that the piglets were frightened, as indicated by piloerection, vasoconstriction and freezing in a tense position. Scan samples showed that the piglets spent an average of 83 per cent of the first day lying down.

None of the piglets learned to feed from the nipple drinker by

themselves. When a piglet fortuitously prodded its nose at the nipple, it did not get any milk, as either there was none present or the nipple was not pushed hard enough to obtain milk. Therefore, the piglets had to be handled in order to encourage them to drink, but this resulted in rapid vocalization and attempts to escape out of the open window. The length of time taken for the focal piglets to start to drink from the nipple on their own varied from seventeen to forty-four minutes after introduction to the incubators. Once they had learned to suck the nipple, they learned to associate the sound of valves clicking in the feeding system with the imminent arrival of an hourly feed. When these clicks were heard they would stand listening, suck the nipple and give whines and squeaks.

2 The first week in the incubators

During this week, fourteen out of the forty-eight piglets under observation died, including the twelve focal animals. Many of the other piglets were unwell, as shown by scouring, weakness and lack of appetite. Four piglets died the day after a malfunction of the heating system, perhaps already weakened by lack of food and *E. coli* infection. Some piglets did not get enough food because, although willing to suckle, as indicated by their expectant waiting at the nipple when clicks were heard, their nipple drinkers were continually getting blocked with dried milk, and they had to wait until someone came and unblocked them. This was especially common for piglets I5, I15 and I17, who developed the habit of screaming loudly and pushing their noses at the window when people were nearby. They also had low growth rates, increasing in weight by less than one kilogram in their first week, whereas none of the piglets with

high growth rates (> 1 kg per week) performed high levels of high-pitched vocalization. Other piglets with low growth rates tended to be weak, resting most of the time and making no effort to go to the nipple drinker at feeding times.

A number of behaviour patterns were performed at significantly higher or lower mean frequencies in the incubators than the Pig Park between one and eight days, and these are shown in Table 2.3. A full list of frequencies and ranges of behaviour patterns performed in the incubators is given in Appendix D. Appendix B gives comparable figures for the Pig Park.

Table 2.3 Behaviour patterns performed at a significantly higher or lower mean frequency in the incubators than in the Pig Park (1-8 days)

Higher in the incubators	Significance $p < 0.05$* $p < 0.001$ **	Lower in the incubators	Significance $p < 0.05$* $p < 0.001$**
lie on belly[a]	**	sit (apart, contact)	**
lie on side[a]	**	stand (apart, contact)	**
slip, fall	*	step, walk	**
whine	*	trot, gallop	**
squeak	*	scamper	**
sniff object	*	hop	**
chew	*	pivot	*
eat food/eat from trough	**	toss head	*
root	**	slow grunting	**
		rapid grunting	**
		sniff floor/ground	**
		paw	*
		suck nipple drinker/teat	**

[a] The significant differences shown here concern the number of 30 second intervals in which these behaviour patterns occurred. The absolute number of times with which transitions to and from lying on the belly occurred in the Pig Park was significantly higher than that in the incubators ($p < 0.001$)*. No significant difference in frequency existed for lying on the side. The values for lying apart and in contact in the Pig Park were combined for comparison with lying in the incubators, where contact was not possible.

*($x^2 = 474.03$; d.f. = 3; $p < 0.001$)

3 The second and third weeks in the incubators

In this period, scan samples indicated significant reductions in the amounts of lying and standing, compared with the first week, along with increases in eating (dried-up milk, and later, milk pellets), drinking, grunting and sucking, biting and massaging the nipple drinker. Table 2.4 indicates behaviour patterns performed at significantly higher and lower frequencies in the incubators versus the Pig Park during this period. A number of abnormal behaviour patterns had now developed. A behaviour pattern never observed in the Pig Park, but occurring at a mean frequency of 3.16 times per half hour in the incubators, was that of nosing and chewing at the forelegs and feet. It was usually performed while in a lying or seated position, and sequence analysis showed that it occurred in significant transitions with slow grunting, chewing (food), rooting and sniffing the floor. Another behaviour pattern occurring during this period, which was abnormal in both frequency and orientation, was the massaging of the nipple drinker and area of window around it. This behaviour is normally directed towards the piglet's own teat on the sow's udder.

As found during the first week, high-pitched vocalizations were associated with frustration of the desire to feed, and occurred at significantly higher levels in the incubators than in the Pig Park. Screaming was rare in the Pig Park, occurring only when a piglet was being crushed or handled, or when it was unable to suck its teat as a result of competition from another piglet or the inaccessibility of its teat. Such high-pitched vocalizations were highest in piglets with low growth rates, but factors other than hunger, such as health and degree of activity, probably also influenced the

Table 2.4 Behaviour patterns performed at a significantly higher or lower frequency in the incubators than in the Pig Park (9-17 days)

Higher in the incubators	Significance $p < 0.05$* $p < 0.001$**	Lower in the incubators	Significance $p < 0.05$* $p < 0.001$**
lie on belly[a]	**	stand (apart, contact)	**
lie on side[a]	**	step, walk	**
sit (apart, contact)	**	trot, gallop	**
alert stance	*	scamper	**
slip, fall	**	hop	**
crawl on belly	*	rapid grunting	**
toss head	*	quack	*
flop	*	wag tail	**
whine	**	urinate	*
scream	*	defecate	*
yawn	*	sniff floor/ground	**
sneeze, cough	*		
stretch	*		
headshake	**		
sniff object	*		
bite object	**		
root, lever	**		
eat food/eat from trough	**		
chew	**		
paw	**		
suck, massage nipple drinker/teat	**		
drink milk (from nipple drinker/teat)	*		

[a] These significant differences concern the number of 30 second intervals in which lying on the belly and side occurred (both apart and in contact in the Pig Park)

vocalization rate. Behaviour patterns involved in significant first-order transitions with whining, squeaking and screaming included stepping, walking, standing, kneeling, slow grunting, eating food, rooting, sniffing the window and pushing at the window.

The piglets in the incubators also showed abnormally high levels of lying on the belly, lying on the side, sitting and kneeling. They almost always rested in contact with the wall, whereas in the Pig Park, an average of 88 per cent of the resting time was spent in contact with other pigs. Comparing positively significant transitions involving sitting (Figure 2.2), it is evident that many more behaviour patterns were frequently associated with sitting in the incubators than in the Pig Park. The same was true for lying.

Other behaviour also occurred at abnormally high rates in the incubators. The piglets often stood leaning against the wall whereas in the Pig Park, leaning only occurred briefly in association with rubbing the side against a tree. Slipping on the floor was significantly more common than slipping on the ground in the Pig Park, and the floor was responsible for the appearance of sores on the knees of five of the piglets. Headshaking was another behaviour pattern more common in the incubators, and often occurred after getting milk on the head while suckling.

In the Pig Park, biting and levering were directed at tree branches, bark, roots and unusual objects, and rooting involved digging into the earth. In the incubators, biting at the trough edge and nipple drinker, and rooting at the floor and trough were performed in a stereotypic manner, being repeated over and over again, often while in a lying or sitting position. Figure 2.3

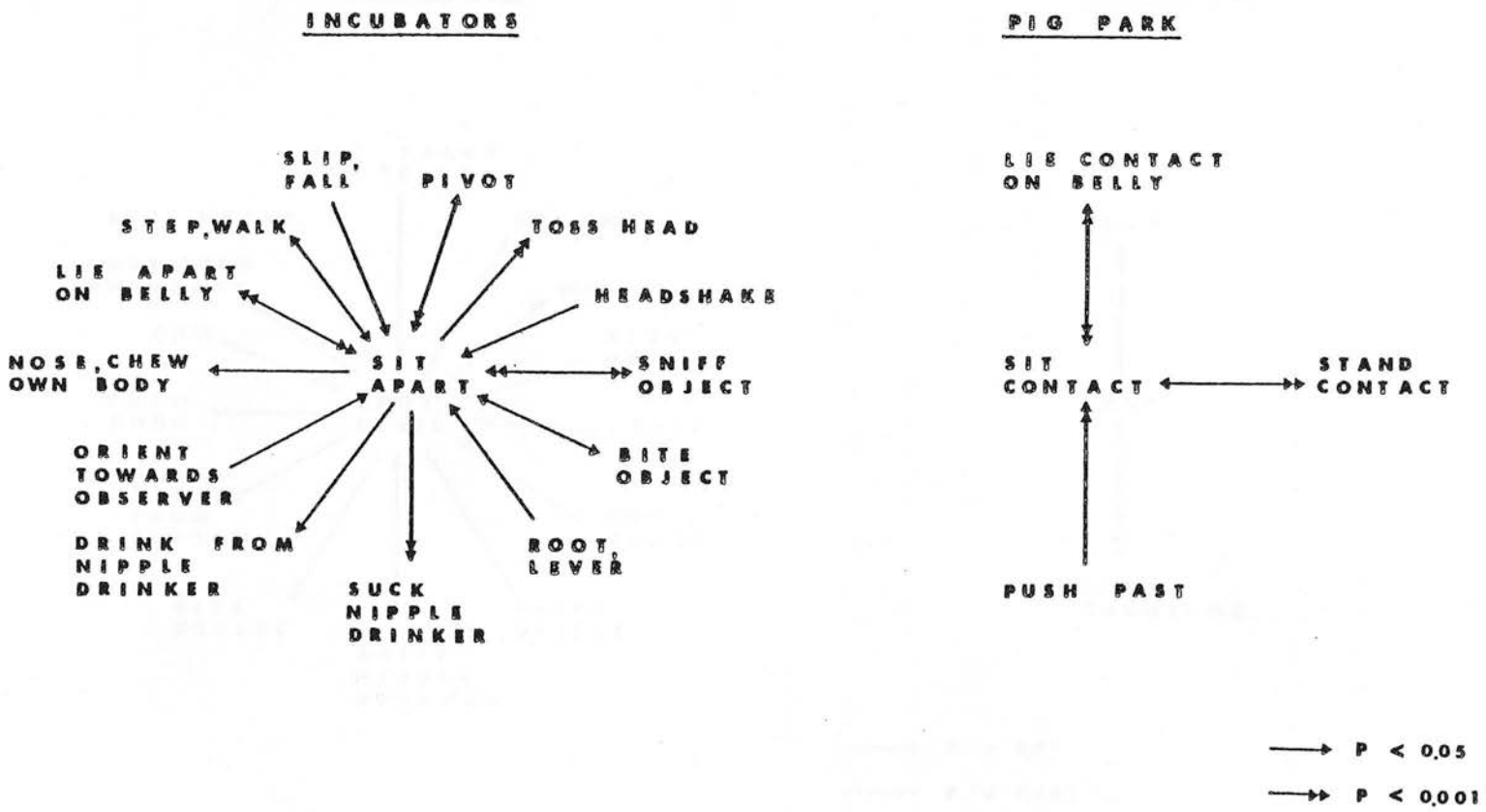

Figure 2.2 Significant transitions involving sitting; 9-17 days

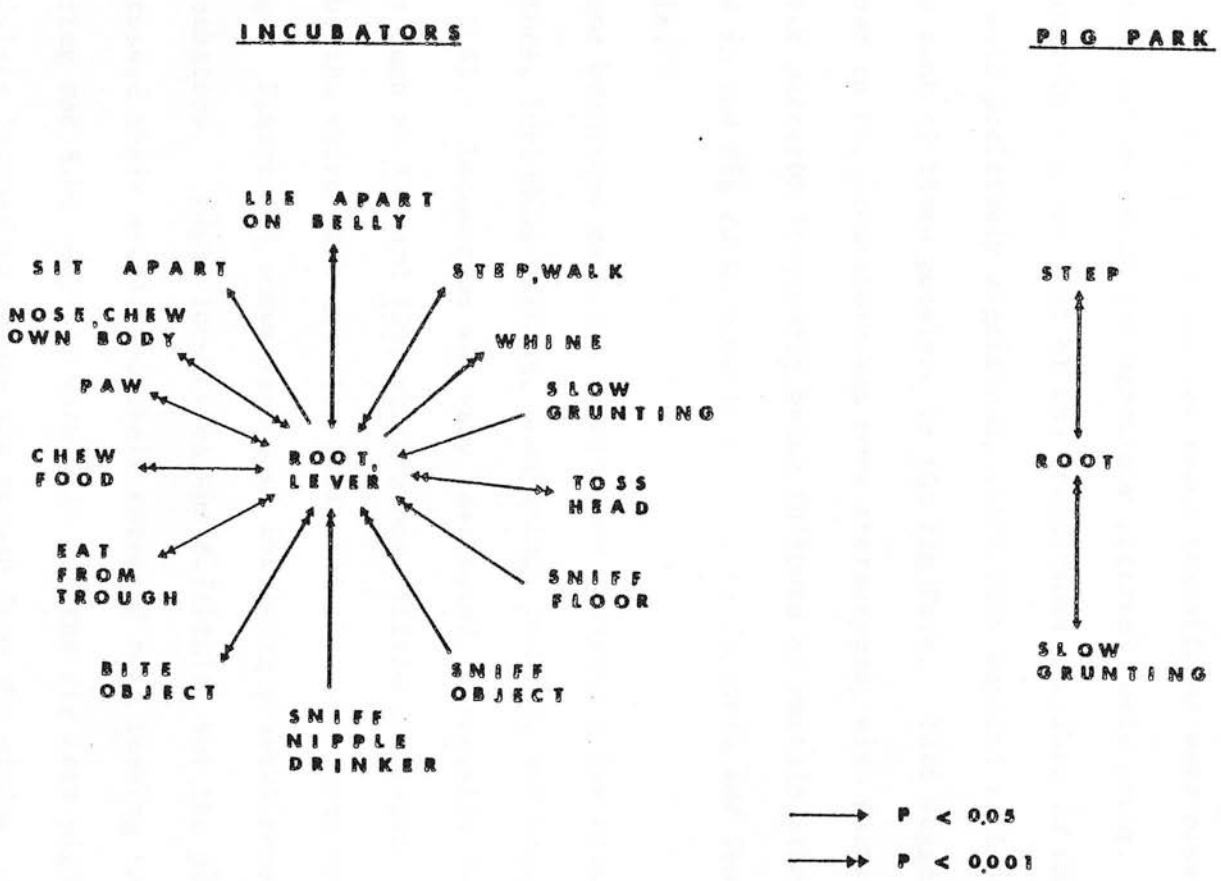

Figure 2.3 Significant transitions involving rooting and levering; 9-17 days (Levering was not recorded in a focal sample in the Pig Park at this age)

shows significant transitions involving rooting and levering in the incubators and Pig Park. A full list of significant transitions occurring in the incubators during this period is given in Appendix E.

When all positively significant transitions between pairs of behaviour patterns are considered, far more occurred in the incubators than the Pig Park and yet fewer transitions were possible in the incubators as no social behaviour patterns could occur. Approximately six per cent of the transitions possible in the incubators were positively significant while this applied to less than one per cent of those possible in the Pig Park. This suggests that behaviour in the incubators was more stereotyped, with particular behaviour patterns frequently being followed by certain others, whereas in the Pig Park, behaviour was more flexible and less predictable.

Some behaviour patterns occurred at abnormally low rates in the incubators, including walking, scampering, grunting and wagging (Table 2.4). Locomotion was very restricted, especially for large piglets such as I18 and I20, which almost filled the entire incubator by the third week and also performed the most lying and sitting. Figure 2.4 shows sequences involving playful movements in the incubators. Rapid locomotion was difficult, but the piglets often tossed their heads, and their ratio of head tossing to scampering was 8.00 compared with 0.14 for the Pig Park piglets. Some piglets learned to remove the trough from the window, and then used it as a toy, pushing it around the incubator and levering, butting and chewing it. Behaviour patterns occurring to a significant extent in play bouts along with the play markers included

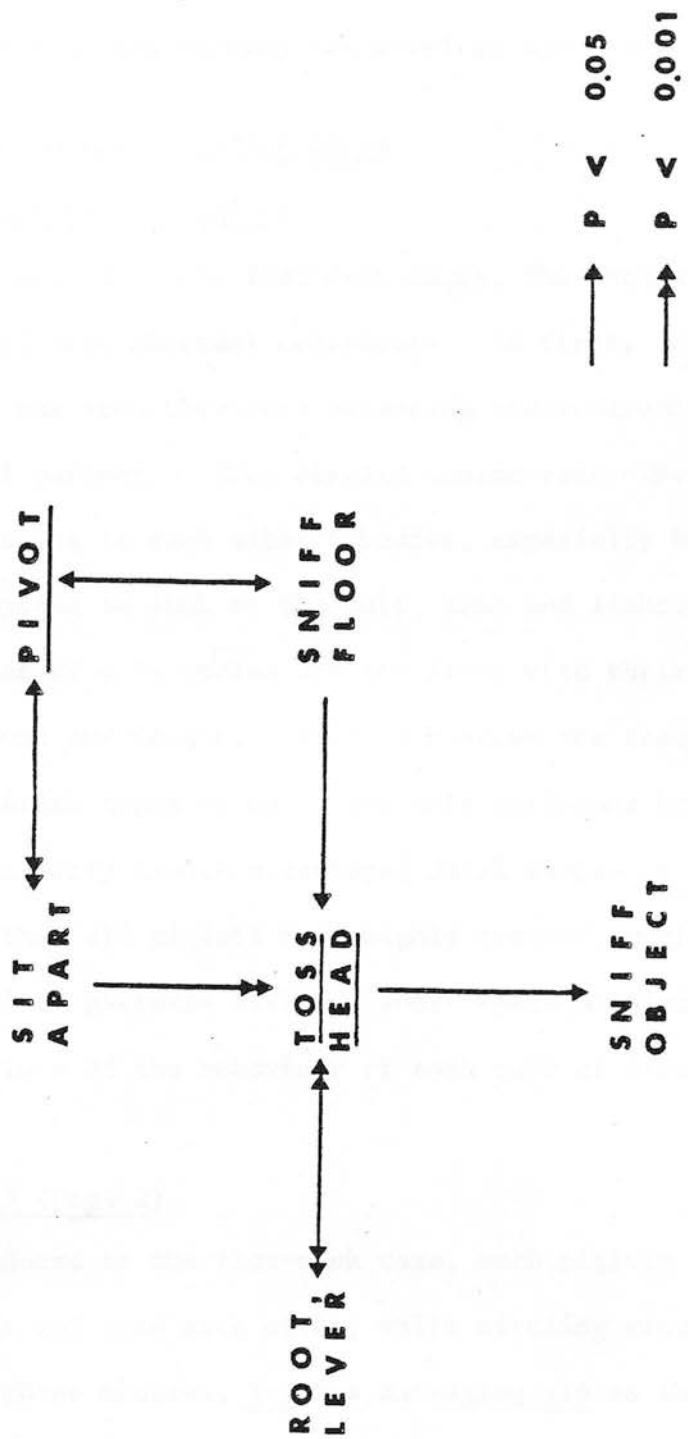

Figure 2.4 Significant transitions involving play markers (underlined) in the incubators; 9-17 days
(see Fig. 1.36 for those occurring in the Pig Park)

sitting apart, wagging the tail, rubbing the head and wiping it across the floor, rubbing the body, sniffing the floor, walls and ceiling, biting fixtures such as the trough and air vent, levering the trough and nosing and chewing the forelegs and feet.

4 Introduction to the flat-deck cages

The incubator-reared piglets

When first placed in the flat-deck cages, the incubator-reared piglets displayed very abnormal behaviour. At first, they walked around the cage but soon they were orienting their attention towards their new social partner. They circled around each other while vigorously massaging at each other's bodies, especially behind the ears, and attempting to suck at the ears, tail and limbs. They also levered each other's bodies off the floor with their snouts, attempted to mount and fought. Table 2.5 shows the frequencies with which different types of behaviour were performed by the focal animals during a forty minute videotaped focal sample of each pair. It was evident that all piglets were highly aroused, performing many different behaviour patterns within a short space of time. A brief account now follows of the behaviour of each pair of incubator-reared piglets.

I16 and I17 (Cage 2)

When introduced to the flat-deck cage, both piglets immediately started to sniff and nose each other, while circling around in contact. Within three minutes, I17 was massaging I16 as they circled around each other. After eight more minutes, I16 became the dominant massager and also kept trying to suck I17's ears, while I17 frequently levered I16's forequarters off the floor. Fifteen minutes later, both were attempting to mount the other's back while

Table 2.5 Frequencies of behaviour patterns performed by the incubator-reared piglets over a forty minute period on their first day in the flat-decked cages

Cage number		Frequency (time/30 minutes) 1		2		3[a]		4	
Interval from introduction to observation (hours)		1		0		0		6	
Focal piglet		I18	I19	I16	I17	I8	I22	I20	I21
Social behaviour	sniff partner	43.0	37.0	9.0	26.3	43.3	18.0	27.3	18.0
	turn away	1.5	1.5	3.8	23.3	10.0	1.8	0.0	0.0
	mount	0.0	2.8	0.0	0.0	0.0	0.8	0.0	0.0
	attempt to mount	9.8	3.8	3.0	3.8	0.0	0.8	0.0	0.0
	circle, bite, knock	26.3	27.0	57.0	44.3	14.8	14.0	0.7	6.0
	shove	4.5	16.3	0.0	0.8	2.0	2.0	0.0	1.5
	lever	0.8	2.3	0.8	3.8	4.8	27.3	0.8	35.3
	suck	0.8	3.8	17.3	0.8	2.8	0.8	23.3	27.0
	massage	3.0	48.5	78.0	44.3	2.8	6.0	20.3	99.0
non-social behaviour	sniff cage	26.8	35.5	1.5	5.3	46.8	14.0	4.5	9.8
	contact with nipple drinker	19.3	23.0	0.8	0.8	6.8	6.0	11.3	11.3
	climb, jump up wall	0.0	0.0	0.0	0.0	9.8	8.0	0.0	0.0
	eat food	no food available		8.3	8.3	16.0	16.8	21.8	42.0
	rub, scratch, headshake	14.5	16.5	4.5	3.0	6.8	14.0	7.5	12.0
	play markers	2.3	20.8	0.0	0.0	0.8	3.3	0.0	5.3
	stand in contact, lie down	33.8	18.8	3.0	1.5	18.8	6.0	4.5	1.5
Percent of minutes spent lying resting		0.0	0.0	0.0	0.0	4.5	0.0	0.0	0.0

[a] The piglets in this cage were observed upon introduction to each other, but both had previously spent 24 hours in flat-deck cages with different partners

continuing to massage the ear and neck region, and when given food, I17 attempted to eat while I16, between grabbing mouthfuls of food, massaged and sucked his ears. By the end of the observation session, both had left the food and were circling around, pushing each other and massaging.

I18 and I19 (Cage 1)

When observed one hour after introduction, this pair had eaten all of their food, and I19 was walking around the cage and sniffing the floor while I18 drank from the nipple drinker. I18 then followed I19, sniffing him and resting his chin on his back. I19 circled around and started to massage I18's side, and then became playful, hopping around and bumping into I18, who was walking around sniffing the nipple drinker, rooting at the floor and biting at the edge of the trough. Then I18 circled around in contact as I19 massaged his side and mounted it, but when I19 sucked his ear, he bit him and was bitten back. This led to a brief fight (20 seconds) with circling, pushing and biting until both walked apart and I18 drank while I19 shook his head and scratched himself with his hindleg. I19 now urinated and I18 gave him an anogenital sniff. Then I19 became playful again and bumped into I18, and then continued to massage his side vigorously, mount him and chew at his legs while I18 seemed to be tired and kept circling around, trying to maintain contact and leaning against his partner. Both made frequent contacts with the nipple drinker and other parts of the cage.

I20 and I21 (Cage 4)

This pair had recently been fed, and ate and drank frequently during their observation session. They also followed each other

around the cage, massaging at their hindquarters and attempting to suck their tails. I21 was most persistent in this activity, and often levered I20's hindquarters into the air, probably in an attempt to get at his tail, which was held down between his legs. When fly killer was sprayed around the room, I21 playfully tossed his head, hindleg scratched and scampered, while I20 went for a drink and then rubbed his side against the wall. They then circled around pushing heads as I21 mouthed at I20's head. After this, I21 continued his massaging and levering activity while I20 kept turning his head towards him, apparently trying to keep his hindquarters away from him.

I8, I9 and I22 (Cage 3)

After twenty-four hours in the flat-deck cage, I9 was very weak, and kept walking away from I8, who continually pursued her, massaging and sucking at her ears. As she was unlikely to survive for long under these conditions, she was removed and replaced by I22. When I22 was introduced, I8 sniffed towards her, went for a drink, and then followed her, levering up and massaging her hindquarters as she walked around the cage. I22 then turned and circled around with I8, who attempted to massage and suck her ears, and followed her as she started to scream and climb the cage walls. Then I8 also started to climb the walls while giving whines and screams, but showed signs of fatigue, and sat leaning against I22 whenever she stood still. She then ate some food, and I22 now started to lever and massage her hindquarters between eating and climbing the walls. At this point I20 and I21 (in Cage 4) had a vigorous fight (circling and biting), and I22 became playful and

bumped into I8 and then continued to massage and lever her. I8 turned and bit at her, and they fought for about ninety seconds before I22 mounted I8's side, who now ran away chased by I22, snapping at her flanks. I8 then sat down in a corner to rest while I22 walked around the cage wagging and headshaking.

The sow-reared piglets

Table 2.6 shows the frequencies of the different behaviour patterns performed by these piglets. Unlike the incubator-reared piglets, whose behaviour was mainly oriented towards each other, these piglets spent most of their time pacing around the cage giving frequent vocalizations, attempting to jump out of the cage and lying resting. No food was available during these observations.

S3 and S4 (Cage 6)

This pair of littermates, which were observed upon introduction to the cage, made frequent transitions between walking, turning, standing and backing up. They also made numerous nose contacts with the cage walls, floor, food trough and nipple drinker. S4 was active throughout the observation session, grunting, screaming and attempting to jump out of the cage. Most of his behaviour was oriented towards the corners and wall between Cages 5 and 6, and he frequently stood listening, with his nose pointing up a corner before climbing up in it. S3 grunted rapidly for the first eleven minutes and climbed the walls several times during this period. Some aggression occurred when both piglets were side-by-side looking up the wall, and this involved parallel pushing of heads and the shoving of S3's head by S4. S3 lay down to rest in a back corner by himself, thirty-four minutes after introduction to the cage.

Table 2.6 Frequencies of behaviour patterns performed by the sow-reared piglets over a forty minute period on their first day in the flat-deck cages

Cage number		Frequency (times/30 minutes) 5		6		7		8	
Interval from introduction to observation (hours)		3		0		1		2	
Focal piglet		S1	S2	S3	S4	S5	S6	S7	S8
Social behaviour	sniff partner	1.5	0.8	0.8	2.3	2.3	0.8	2.3	0.8
	turn away	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0
	mount	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0
	attempt to mount	0.0	0.0	1.5	0.8	0.0	0.8	0.0	0.0
	circle, bite, knock	0.8	0.0	1.5	0.0	3.8	2.8	1.5	2.3
	shove	0.0	0.8	0.8	5.3	0.0	0.8	0.0	0.8
	lever	0.0	0.0	0.0	0.8	0.8	0.0	0.8	0.0
	suck	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	massage	0.0	0.0	0.0	0.8	0.8	0.0	3.8	0.0
Non-social behaviour	sniff cage	1.5	3.0	96.0	75.0	18.0	23.3	25.5	5.3
	contact with nipple drinker	0.8	1.5	5.3	3.8	0.8	1.5	1.5	0.0
	climb, jump up wall	0.0	0.0	29.3	3.0	5.8	6.8	0.8	0.0
	eat food	no food available							
	rub, scratch, headshake	2.3	0.0	0.0	0.8	0.0	1.5	0.8	0.0
	play markers	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	stand in contact, lie down	9.8	9.0	10.5	3.8	24.8	13.5	18.8	15.8
Percent of minutes spent lying resting		90.0	70.0	0.0	15.0	78.0	78.0	67.5	85.0

S5 and S6 (Cage 7)

When observations on these littermates started, an hour after introduction, both were making frequent transitions between locomotion, standing, sniffing the cage and climbing the walls. S5 gave frequent long, high squeaks while S6 grunted periodically. S5 urinated in the trough, which became the habit of both piglets for the remainder of the study. They first lay down seventy-nine minutes after introduction, and some knocking and parallel pushing of heads occurred when S6 attempted to lie on top of S5's back. After lying apart for two minutes, S6 moved to lie in contact with S5, where they remained until the end of the observation period, grunting occasionally.

S7 and S8 (Cage 8)

This pair of non-littermates fought vigorously fifteen minutes after introduction. When observed after two hours, they were lying resting in contact. S7 then started walking along the walls screaming, while S8 stepped around the cage grunting and stood in contact with S7, and then lay down again by herself. S7 sniffed noses with S6 (a non-littermate) through the wire mesh of the cage wall, and then rooted along S8's side looking for a place to lie down. S8 knocked at her, both stood up, S7 lay on top of her and then they lay down beside each other, in contact with S5 and S6 on the other side of the wall.

S1 and S2 (Cage 5)

These non-littermates fought an hour and ten minutes after introduction, and were observed after three hours. S1 had been lying resting alone for most of this time while S2 had been very

active, screaming and jumping up the wall. During the observation session, S2 walked back and forth along the walls, stopping frequently, and continuously grunting, screaming and whining, while S1 rested for all but four minutes.

5 Behaviour from the second to the tenth day in the flat-deck cages

During this period, when the piglets were between eighteen and twenty-seven days old, the incubator-reared piglets showed a much higher level of activity than they had in the incubators. A comparison of the number of scans in which different behaviour patterns were performed between nine and seventeen days in the incubators, and eighteen and twenty-seven days in the flat-deck cages indicated significant increases in locomotion, eating, drinking, standing and elimination and a reduction in the level of behaviour oriented towards the nipple drinker. When compared with the sow-reared piglets, they performed significantly more shoving, circling, massaging, levering, sniffing and sucking (the ears) and significantly less lying, vocalizing, knocking, chewing (food), sniffing the floor and biting objects (Table 2.7). Both incubator-reared and sow-reared piglets exhibited numerous differences in behaviour when compared with the Pig Park piglets at this age. For example, they performed more high-pitched vocalizations, comfort movements, urination, drinking, eating, circling, levering, sniffing, massaging, sucking and mounting and less scampering, grunting and lying in contact (Table 2.8). Appendix D gives the frequencies of all behaviour patterns performed by the incubator-reared piglets and sow-reared piglets during this period.

A number of behaviour patterns were performed at a

Table 2.7 Behaviour patterns performed in the flat-deck cages at a significantly higher or lower frequency by the incubator-reared piglets than the sow-reared piglets (18-27 days)

Higher in the incubator-reared piglets	Significance $p < 0.05$* $p < 0.001$**	Lower in the incubator-reared piglets	Significance $p < 0.05$* $p < 0.001$**
scamper	*	lie apart on belly	**
scratch	*	stand apart	**
root	**	alert stance	*
drink water from nipple drinker	*	slow grunting	**
sit contact	*	rapid grunting	**
push heads, parallel	**	whine	**
circle	**	squeak	**
shove head, body	**	squeal	*
lever body	**	orient towards observer	*
sniff head, noses	**	sniff floor	*
sniff body	*	bite object	*
suck, chew head	**	chew (food)	*
massage nipple drinker	**	lie contact on belly	**
massage head	**	knock	*
massage body	**		

Table 2.8 Behaviour patterns performed at a significantly higher or lower frequency in the flat-deck cages than the Pig Park (18-27 days)

Higher in the flat-deck cages	Significance $p < 0.005$* $p < 0.001$** Incubator-reared v Pig Park piglets	Sow-reared v Pig Park piglets	Lower in the flat-deck cages	Significance $p < 0.05$* $p < 0.001$** Incubator-reared v Pig Park piglets	Sow-reared v Pig Park piglets
lie apart on belly	*	**	trot, gallop	**	**
sit apart	*	*	alert stance	**	*
stand apart	**	**	scamper	**	**
step, walk	**	**	rapid grunting	**	*
climb	**	**	lie contact on belly	**	*
whine, squeak	**	**	lie contact on belly (refers to No. 30 second intervals)	**	*
scream	**	**			
wag tail	**	**			
yawn	**	**			
stretch	*	**			
headshake	**	**			
scratch	**	**			
rub body	**	*			
urinate	*	*			
sniff objects	**	**			
bite objects	**	**			
drink water	**	**			
eat food	**	**			
chew	**	**			
kneel contact	*	*			
stand contact	**	**			
circle	**	**			
lever body	**	**			
sniff head, body	**	**			
suck, chew head, body	**	**			
attempt to mount, mount	**	**			
massage head, body, belly/ suck, massage teat	**	**			

significantly higher rate by one member of a pair of piglets than by its partner, and these are listed in Table 2.9. Because the piglets were kept in pairs, more avoidance was observed between particular dyads than in the Pig Park. Therefore, dominance relationships were clear in most cases, as one member of the pair (the subordinate) was significantly more likely to turn away from its partner than *vice versa*. From Table 2.9 it can be seen that piglets I8, I16, I19, S1, S3 and S5 were subordinates during this period, while there were no obvious dominance relationships between S7 and S8 or between I20 and I21. Piglet I16 became ill by her second day in the flat-deck cages, and received a high level of massaging and sucking of her ears from her partner, I17, while she lay or stood with her nose resting on the floor. By the fourth day, I17 was also sick, and both lay resting for a significantly large proportion of the time until they died, on the sixth (I16) and tenth (I17) day. They rested in 79.80% and 69.23% of scans, respectively, versus 48.70% of scans for all incubator-reared piglets combined, between the fourth and tenth day in the flat-deck cages ($\chi^2_k = 23.50$; d.f. = 2; $p < 0.001$). I18, who had performed a high level of massaging of the nipple drinker in the incubators, now redirected this behaviour towards the nipple drinker and wall behind it in the flat-deck cages. Piglets I20 and I21 performed high rates of circling, and levering up each other's hindquarters during this period.

6 Behaviour after ten days in the flat-deck cages

During this period, when the piglets were twenty-eight to forty-one days old, it was notable that the initially high rates of massaging, sucking and levering the partner had declined

Table 2.9 Behaviour patterns performed at a significantly higher frequency by one member of a pair than its partner (18-27 days old)

Cage number	Piglet	Behaviour patterns performed at a higher rate ($p < 0.05$) than partner
1	I18	slow grunting, whine, bite objects, root, massage nipple drinker
	I19	stand apart, step/walk, wag, eat, chew, shovel, scamper, pivot, toss head, turn away, sniff body
2	I16	lie apart on belly, stand apart, walk, turn away
	I17	massage head/body, lever body, sniff head/body, suck head, shove head
3	I8	step, chew, sniff head/body, massage body, turn away
	I22	trot, paw, bite objects
4	I20	eat, chew
	I21	stand, slow grunting, whine, massage body, suck body, lever body
5	S1	lie apart on belly, sit contact, stand contact, step, walk, whine, wag, headshake, sniff floor, sniff objects, chew, root, massage belly, lever body, suck body, sniff head/body, knock, mount side, turn away
	S2	lie contact on side, massage body
6	S3	squeak, sniff floor, eat, chew, root, knock, turn away
	S4	stand apart, slow grunting, massage head
7	S5	kneel apart, climb, squeak, scream, bite objects, sniff urine, lie contact on belly, orient towards partner, mount side, turn away
	S6	slow grunting, rapid grunting, wag, paw, stand contact, suck head, shove head, lever body
8	S7	pivot, slow grunting, squeak, eat, chew, orient towards observer, sniff head/body
	S8	shovel, paw, massage body

significantly in the incubator-reared piglets coincident with increases in these behaviour patterns in the sow-reared piglets. Figure 2.5 shows significant transitions occurring between different types of social behaviour in the incubator-reared and sow-reared piglets in the flat-deck cages and the piglets in the Pig Park when they were eighteen to twenty-seven days old versus twenty-eight to forty-one days old. It is evident that social transitions were performed far more frequently in the flat-deck cages than in the Pig Park, and that the social behaviour of the incubator-reared and sow-reared piglets was becoming more alike with increasing time in the flat-deck cages. In fact, scan samples showed no significant differences between the behaviour of the two groups at the later age, with the exception that the incubator-reared piglets performed more climbing, massaging the nipple drinker and eliminating, while the sow-reared piglets showed higher levels of lying, locomotion and high-pitched vocalization. However, the more sensitive focal sampling technique showed up additional differences (Table 2.10). The incubator-reared group performed more massaging of the head, especially around the ears, while the sow-reared piglets were more likely to massage their partner's belly, which was sometimes invited by lying on the side to expose the belly. The incubator-reared piglets performed more mounting, but both groups mounted from the side more often than from the rear and both males and females mounted their partners. The sow-reared piglets were more likely to sniff and chew at their partner's body, putting their mouths around any protrusion, especially the legs and the hip bone, and this behaviour appeared to be a form of manipulation of the environment rather than redirected suckling behaviour.

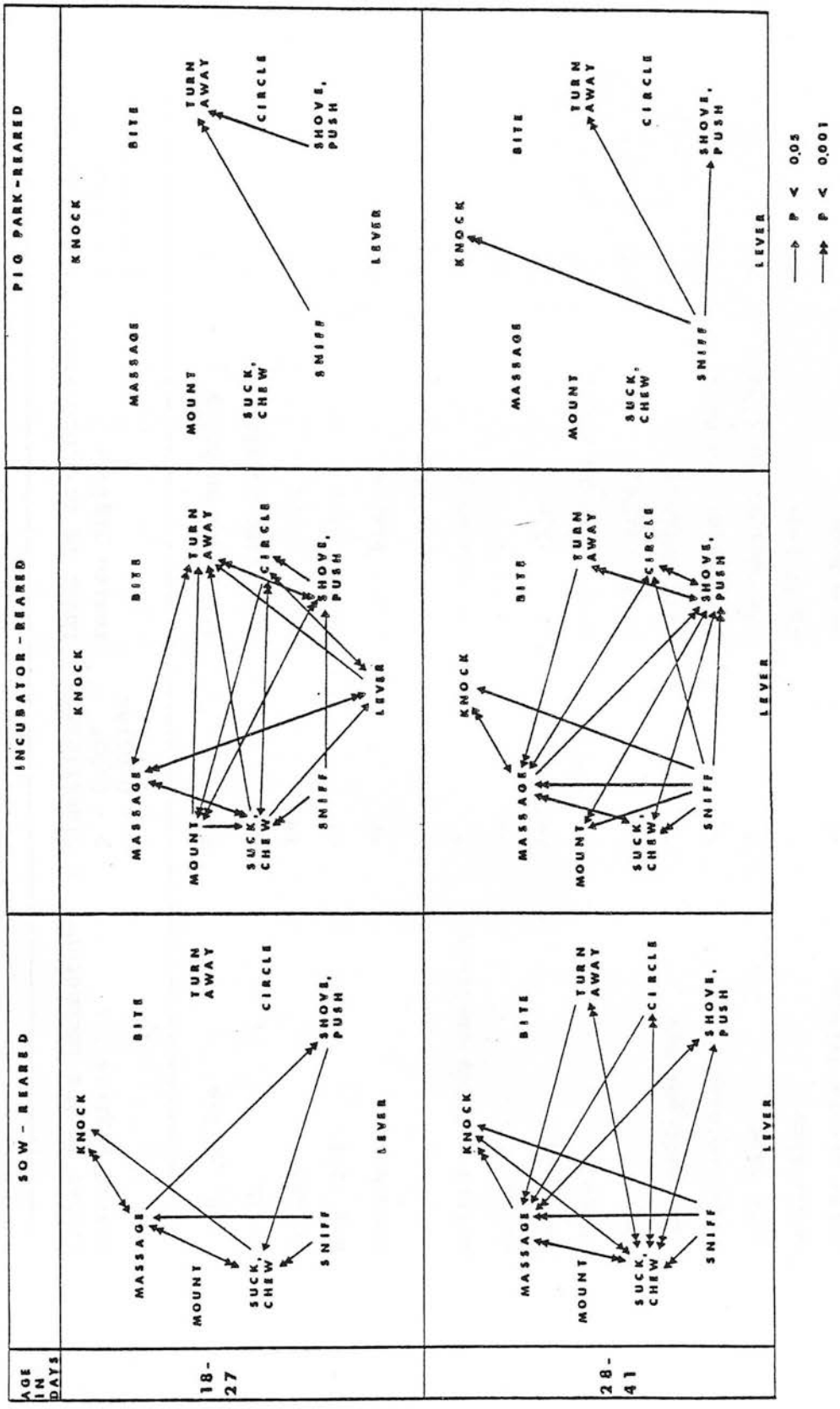

Figure 2.5 Significant transitions between social behaviour patterns in different rearing systems at two different ages
(Mount includes attempt to mount, sniff includes orient towards. All patterns include giving and receiving the behaviour.)

Table 2.10 Behaviour patterns performed in the flat-deck cages at a significantly higher or lower frequency by the incubator-reared piglets than the sow-reared piglets (28-41 days)

Higher in the incubator-reared piglets	Significance $p < 0.05$* $p < 0.001$**	Lower in the incubator-reared piglets	Significance $p < 0.05$* $p < 0.001$**
trot, gallop	*	lie apart on belly	**
climb	**	lie apart on side	*
scream	**	kneel apart	**
wag tail	**	stand apart	*
headshake	**	alert stance	*
scratch	*	slow grunting	*
orient towards observer	*	sneeze, cough	*
drink water	**	stretch	*
eat food	**	sniff floor	**
shovel	*	walk sniffing floor	*
paw	*	sniff urine	**
push past partner	*	bite objects	**
stand contact	**	lie contact on belly	**
turn away	*	lie contact on side	*
mount side	*	sniff body	*
sniff nipple drinker	**	chew body	*
massage nipple drinker	**	anogenital sniff	*
massage head[a]	**	massage belly	*

[a] Refers to number of 30 second intervals. There was no significant difference in the absolute number of times it was performed by each group.

Concerning dominance relationships in this period, only I8, S5 and S7 were significantly likely to turn away from their partners. This is in keeping with the finding in the Pig Park that dominance relationships were ill-defined between familiar piglets and did not prevent them from engaging in social interactions.

An interesting habit observed only in the incubator-reared piglets was that of running back and forth between the food trough and the nipple drinker when fed, and this no doubt contributed to their higher frequencies of trotting, sniffing and drinking from the nipple drinker and eating food. The piglets of each pair alternated their trips to the nipple drinker, and fighting over possession of the drinker was never observed. Figure 2.6 shows an example of feeding and drinking behaviour in an incubator-reared and a sow-reared piglet. Comparing results from all piglets in each group, the incubator-reared piglets almost always made six or more trips to the nipple drinker for a drink in the first thirty minutes after feeding while the sow-reared piglets were never observed to make more than five trips.

Massaging around the nipple drinker was now performed at a high rate by I18 and I20, and to a lesser extent by their partners. Characteristic positions were taken up while performing this behaviour, with I18 always standing at an angle to the right of the drinker while I19 stood to the left. I20 usually sat while massaging and resting his nose on the nipple drinker, and I21 lay to his left, massaging behind his ear or resting his head on I20's back. Although the sow-reared piglets occasionally made one or two movements of the nose up and down the wall by the water nipple, they were never observed to spend long periods massaging.

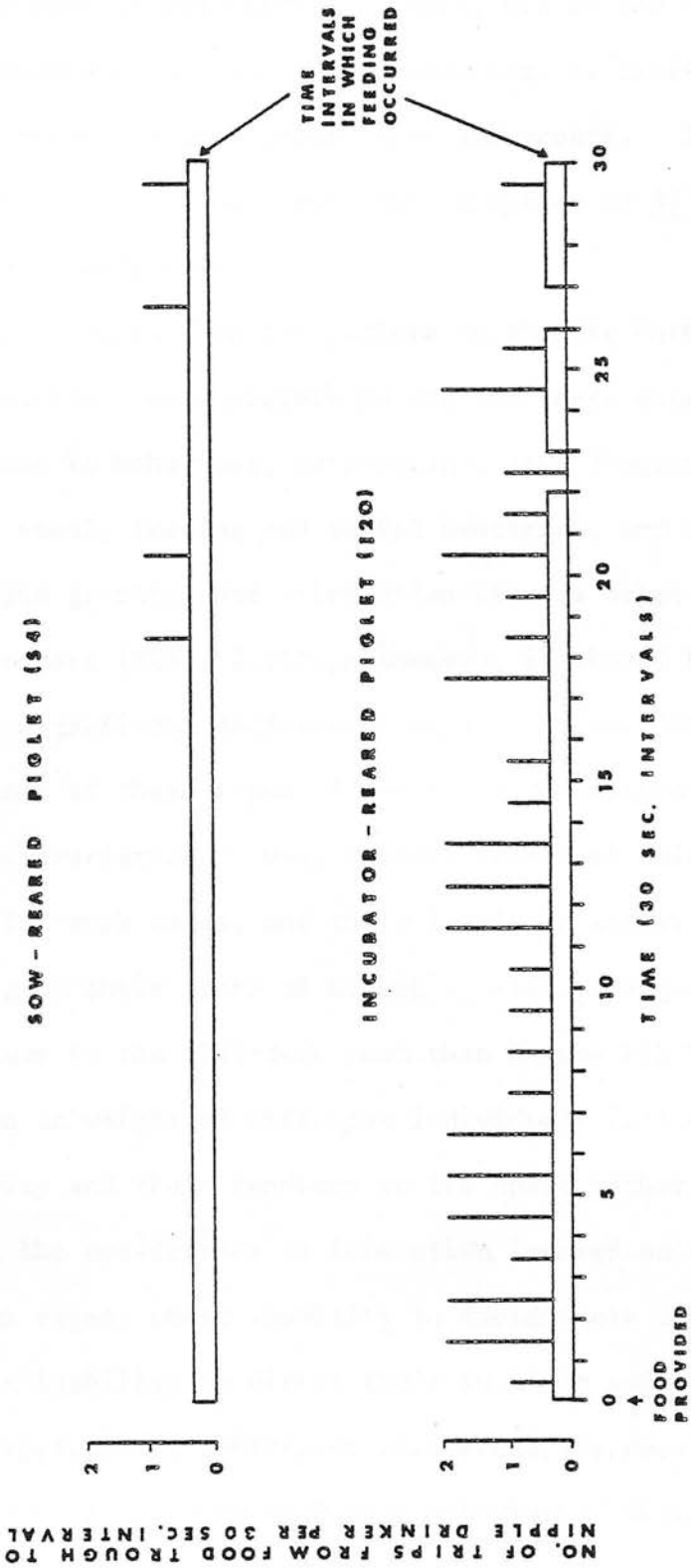

Figure 2.6 Examples of feeding and drinking behaviour in the Flat-Deck cages

Appendix D gives complete lists of the frequencies of behaviour patterns performed during this period. It should be noted that, by the third week in the flat-deck cages, all of the incubator-reared piglets showed signs of *E. coli* infection, as manifested by puffy cheeks, sunken bellies, greasy skin and scours. The sow-reared piglets remained healthy, with the exception of S7 and S8, which got scours and grew poorly.

When compared with the piglets in the Pig Park, both incubator-reared and sow-reared piglets in the flat-deck cages showed numerous differences in behaviour, performing higher frequencies of resting, comfort, vocal, feeding and social behaviour, and lower levels of play, rapid grunting and orientation towards other pigs without making contact (Table 2.11). However, it should be noted that, although significant differences existed in the overall levels of performance of these types of behaviour, no allowance was made for individual variation. Only a small number of animals were observed in the flat-deck cages, and their levels of activity varied depending on their state of health. Also, the generally higher temperature in the flat-deck room than in the Pig Park and the variation in weight of different individuals influenced their levels of activity and their tendency to lie apart rather than in contact. Finally, the constraints on locomotion imposed on the piglets in the flat-deck cages, their inability to avoid their urine and faeces, and their inability to direct their suckling and foraging behaviour towards appropriate substrates influenced the results. Therefore, it is hardly surprising that many behavioural differences existed between the piglets in the two environments.

Table 2.11 Behaviour patterns performed at a significantly higher or lower frequency in the flat-deck cages than the Pig Park (28-41 days)

Higher in the flat-deck cages	Significance $p < 0.05$*; $p < 0.001$**		Lower in the flat-deck cages	Significance $p < 0.05$*; $p < 0.001$**	
	Incubator-reared v Pig Park piglets	Sow-reared v Pig Park piglets		Incubator-reared v Pig Park piglets	Sow-reared v Pig Park piglets
lie apart on belly	**	**	trot, gallop	**	**
sit apart	*	**	scamper	**	**
kneel apart	**	**	rapid grunting	**	**
stand apart	**	**	shovel	*	**
step, walk	**	**	lie contact on belly (refers to number of 30 second intervals)	**	**
climb	**	**			
toss head	*	*	orient towards	**	**
bump	**	*			
slow grunting	**	**			
whine, squeak	**	**			
wag tail	**	**			
yawn	*	*			
stretch	**	**			
headshake	**	**			
scratch	**	*			
urinate	*	*			
sniff urine, faeces	**	**			
bite objects	**	**			
root, lever up objects	*	*			
drink water	**	**			
eat food	**	**			
chew	**	**			
paw	**	*			
push past	**	*			
stand contact	**	*			
knock	**	*			
lever body	*	**			
sniff head, body	**	**			
suck, chew head, body	**	**			
attempt to mount	**	**			
massage head, body, belly/ suck, massage teat	**	**			

DISCUSSION

Mortality, illness and injury

Concerning the theoretical advantages of very early weaning, a reduction in the mortality rate of neonatal piglets from that found in conventional rearing systems was not found in this study. In fact, the overall mortality to six weeks of age in a sample of forty-eight piglets was 39.6 per cent (nineteen piglets). It is likely that the fourteen deaths occurring in the first week after birth were the result of lack of nutrition in the first two days (Lecce, 1969); partly from not getting a good dose of colostrum from the sow on the first day and partly from not obtaining enough milk from the nipple drinkers in the incubators. The initial disinterest shown by the piglets towards the nipple drinkers may have been due to a lack of key stimuli which normally facilitate feeding, including a warm, odorous udder with soft, pliable, projecting teats, the continuously available and easily extractable supply of milk on the day of birth, the lactation call of the sow and the presence of other squeaking piglets at the udder. It may be that very young piglets are not aware of a feeling of hunger (Hinde, 1970) and rely on external stimuli to attract them to the nipple. Also, it is possible that fear aroused in the absence of the sow results in behaviour (attempts to escape, lying shivering) which conflicts with behaviour needed in order to learn to feed from a new source. That the sow is already, to some extent, familiar to the piglet by this time is shown by the work of Horrell (1982), who found that day old piglets in a T-maze showed a clear preference for their own mother when given a choice between her and another sow.

Olfactory stimuli from the mother sow were sufficient to cause a response.

Deaths occurring after the first week of life were probably mainly due to infection by *E. coli* as a result of the absence of a continuous supply of immunoglobulins from sow's milk. Lack of disease resistance can be counteracted by keeping piglets in a completely sterile environment, but this is expensive and impractical from the production point of view, although gnotobiotic piglets are reared in this way for research purposes (Noyes, 1976).

It is evident that rearing in individual incubators did not prevent the spread of infection between piglets, and it is interesting that Jeppesen (1980) was able to raise piglets on an artificial sow in groups of four and eight with a mortality rate to seven weeks of only 7.8 per cent (five piglets out of a sample of sixty-four). It is possible that stress caused by rearing in social isolation in incubators may have reduced the piglets' resistance to disease. This is supported by Riley's (1981) finding that socially isolated mice had a much lower ability to reject a tumour challenge than mice kept in groups. However, it is not known how stress is related to disease resistance, and Prohάska (1981) did not find higher levels of blood cortisol (often associated with stress) in pigs infected with *E. coli*. Also, Jeppesen's higher survival rates may have been due to her use of different feeding and hygiene régimes.

There is no doubt that illness and starvation did affect the behavioural results obtained in this study, causing high levels of inactivity in affected piglets. It is likely that ill health was an important variable influencing the development of abnormal

behaviour. In fact, changes in behaviour are often the first indication of internal disorders, and Fraser (1978) has suggested that the unusual behaviour associated with early weaning may be due to digestive upset brought on by a change in diet. This leads to discomfort, restlessness and fatigue.

It is generally accepted that injury, as well as illness, indicates a lack of well-being in an animal. Injury, as a result of living in the incubators, appeared in the form of sores on the knees, obtained from slipping and kneeling on the wire mesh floor which was wet with milk and urine. Although no apparent physical damage resulted from the nosing and chewing of the forelegs seen in the incubators and flat-decks, it is possible that this behaviour could become pathological. Monkeys kept in a very barren environment sometimes lick small wounds so often that they do not heal, but become large 'running sores' (Morris, 1964), while self-grooming by veal calves kept in crates results in the development of harmful hair balls in the abomasum (Webster and Saville, 1981). The high level of abnormal sucking and massaging behaviour observed in both incubator-reared and sow-reared piglets in the flat-deck cages was also potentially harmful. As well as causing stress to the receiver of this activity, by preventing it from resting and feeding undisturbed, it also resulted in red and swollen areas on the body. This is the first stage in the development of necrotic lesions of the skin and underlying muscle, which are found in some piglets after weaning (Allison, 1976). It is also well-documented that excessive nosing and sucking can lead to outbreaks of ear and tail biting in early-weaned piglets (Blackshaw, 1980). In addition to the detrimental effects of this behaviour upon the well-being of the

receiver, the high level of performance of abnormal suckling behaviour is probably a good indication of the lack of well-being of the performer. In this study, the piglets performing the most massaging also had scours and low growth rates, as did the piglets receiving the most massaging. A high level of non-nutritive suckling behaviour has been associated with digestive disorders, poor weight gain and hunger in early-weaned piglets by other workers (Fraser, 1978; Jeppesen, 1980), and Worsaae and Schmidt (1980) found a positive correlation between high levels of non-nutritive oral activity and high blood cortisol levels in early weaned piglets, indicating the presence of stress. It would be most interesting to determine how physiological measures (e.g. plasma cortisol and glucose concentrations, heart rate, body temperature, etc.) are related to the behaviour of piglets reared in individual incubators.

Physical restriction and play

That the piglets were very restricted in their ability to move about in the incubators was indicated by their abnormally low levels of locomotion and high levels of lying and sitting while performing other activities. This had a deleterious effect on the piglets in that, when transferred to the flat-deck cages, they were very stiff, and walked in a bow-legged manner on weak hindlegs. More long-lasting detrimental effects may be inferred. Pittaway and Brown (1974) have reported that an increased frequency of lameness in pigs was due to lack of exercise. If a requirement for exercise exists in piglets, then it will normally be satisfied during bouts of locomotory play. In the incubators, where rapid forward movement was prevented, play was manifested by behaviour patterns normally

occurring at a lower rate, such as tossing the head. This behaviour may have been performed in frustration, as a substitute for rapid locomotion. Playful movements of the head may have strengthened the neck, but exercise of other parts of the body was lacking. Overall, the frequency of behaviour patterns performed during play bouts was significantly lower in the incubators than in the Pig Park. This was probably due to a lack of stimuli facilitating play, such as the presence of other playful piglets, startling movements or sounds and the appearance of novel objects.

When first placed in the flat-deck cages, the piglets did not run around rapidly and playfully, releasing pent-up energy, as might have been expected after a long period of confinement (Lorenz, 1981). For example, Müller-Schwarze (1968) found that young black-tailed deer, *Odocoileus hemionus*, ran faster and for longer after a period of play deprivation, and Chepko (1971) found an increase in play, and in the frequency and duration of activity periods in young goats after play deprivation. However, in these cases, the animals were not being released into a novel environment with novel social companions. Nevertheless, some play did occur in the incubator-reared piglets on the first day in the flat-decks, while none was seen in the sow-reared piglets, and play remained at a higher level in the incubator-reared piglets to the end of the study, although never reaching the levels seen in the Pig Park.

As found in the Pig Park, individual differences in the rates of play performed by piglets in the flat-decks, did not seem to be good indicators of well-being, as some piglets suffering from scours and performing high rates of non-nutritive suckling behaviour also showed relatively high rates of play. Jeppesen (1980) came to the

same conclusion for her artificially-reared piglets, as play was often stimulated by changes in the environment, such as removal of the artificial sow.

The development of stereotypies

After habituation to the barren environments of the incubators and flat-deck cages, the piglets spent long periods in a low state of arousal due to a general lack of stimulation. This probably was an important factor influencing the development of stereotypies, such as rooting or biting at the floor or trough, nosing and chewing the forelegs, head shaking and scratching, and massaging and sucking at the nipple drinker (incubator-reared piglets only) or social companion. These behaviour patterns were repeated monotonously, usually while in a lying, sitting or kneeling position. That the same stereotypies appeared in the sow-reared piglets indicates that early social isolation was not the main causal factor. Rather, the low level of stimulation and the absence of appropriate substrates for the direction of oral and manipulative behaviour, resulted in a generalization of the stimuli able to elicit these types of behaviour. Thus, in the absence of interesting distractions, the slightest irritation of the skin might elicit comfort behaviour. Similarly, massaging behaviour, originally associated with suckling for milk, was redirected towards substrates which had never provided milk, such as the partner's body. In the Pig Park, massaging at the sow's udder was performed much less frequently because when the sow walked off after suckling, or rolled over on her belly, the piglets' attention was soon diverted to other stimuli. In the barren environments, any object which could be moved, such as a loose

trough or cage wall, or the body of the partner, was frequently manipulated, and its ability to move and to make a noise was no doubt rewarding, by increasing the level of stimulation received by the piglet. It is interesting that the incubator-reared piglets, having acquired a stereotyped massaging response in the incubators, later performed this stereotypy at a frantic rate when highly aroused upon introduction to the flat-deck cages. It may be that the performance of a familiar and commonly repeated action, previously associated with a low state of arousal, now occurred in an attempt to reduce arousal.

Reproductive behaviour

The reader is referred to Varley (1982) for a discussion of the problems encountered when attempting to increase the sow's reproductive capacity by very early weaning of the piglets. As far as the piglets were concerned, there was no indication that social isolation had affected their ability to mount. In fact, they showed higher levels of mounting in the flat-decks than the sow-reared piglets. In other ways, mounting was similar to that of the sow-reared piglets and Pig Park piglets, with large individual differences in its rate of performance.

The motivational system controlling mounting was not clear. It was sometimes performed during circle fighting, apparently in an attempt to prevent the partner from circling around and biting the head and neck region. It also occurred in play. As behaviour having a clear sexual motivation does not occur until piglets are over three months of age, it is unlikely that social deprivation, during the first three weeks of life, was as detrimental to the

success of future sexual behaviour as it would have been if occurring after this time or for a longer period. However, further investigation into possible effects of early isolation on adult male and female sexual behaviour is required. Of course, besides housing in isolation, housing in small flat-decks with only one social companion was not conducive to gaining experience in directing sexual behaviour appropriately in the presence of animals of different sexes, sizes and degrees of aggressiveness.

Behaviour directed towards the nipple drinker

The main difference in the behaviour of the incubator-reared piglets versus the sow-reared and Pig Park piglets, concerned the behaviour directed towards the nipple drinkers. The incubator-reared piglets developed a strong habit of spending long periods sucking and massaging the nipple drinkers, presumably due to their association with a milk reward. This probably explains why they continued to direct suckling behaviour towards them when they provided only water, although water may have been rewarding if it alleviated discomfort due to dehydration caused by scouring. It is interesting that when transferred to the flat-deck cages, these piglets made more frequent contacts with the new nipple drinker than the sow-reared piglets. This was probably because it had greater significance to them as a familiar, rewarding object. After habituation to the flat-decks, the incubator-reared piglets performed stereotyped massaging of the nipple drinker, and also ran to it frequently during feeding, suggesting either that some reward was obtained from the performance of this behaviour, or that the piglets had not yet learned that the drinker would no longer supply milk.

The former suggestion seems more likely, as the response persisted even after three weeks in the flat-decks.

Although it was not possible to mix incubator-reared piglets with sow-reared piglets due to the risk of disease, it is possible that the habit of running to the nipple drinker during feeds would have placed the incubator-reared piglets at a disadvantage, because it would have reduced their eating time at the trough and enabled the sow-reared piglets to eat more of the limited supply of food.

Motivational factors influencing behaviour

When the incubator-reared piglets were introduced to the flat-deck cages, it was immediately evident that they had been affected by their previous social isolation. They performed many social behaviour patterns at a frantic rate, and did not seem to be afraid of their new surroundings or their new social partner. They behaved in a manner which suggested that during the period of social isolation, their threshold for reaction to all types of stimuli had been lowered, and their internal motivation to perform socially directed behaviour patterns had been frustrated by the lack of key stimuli from conspecifics which normally elicit their performance. Thus, when suddenly given the chance to interact socially, they did so in a vigorous and prolonged way. It is difficult to interpret their behaviour in terms of motivational states, as many different types of behaviour occurred in a short space of time, but were continually being interrupted by the movement of both piglets of a pair. Whether there was a frequent switching between different motivational states, or whether the general high state of arousal allowed the simultaneous expression of different types of behaviour

is not known. It is likely that high arousal was maintained by an inability to filter out the many novel stimuli bombarding the senses, as a result of previous housing in a barren environment. Therefore, the piglets were unable to concentrate on a specific set of stimuli for any length of time, but were continually being distracted, resulting in incomplete sequences of behaviour directed towards different sets of stimuli. However, the most frequently attempted type of behaviour was the massaging and sucking of the partner's body, and other socially directed behaviour was perhaps incidental. For example, the continuous circling of each piglet around the other may have resulted from trying to get into a suitable position for an uninterrupted bout of massaging and sucking of the partner's ears or tail. This did occur if one piglet remained still for a short period. Circling is normally associated with fighting behaviour (or play fighting if familiar), and it is likely that some aggression was aroused, as some biting did occur. There may have been a desire to dominate the partner, as manifested by persistent hard massaging, levering, pushing and mounting. That aggressive and suckling tendencies can occur in close succession is shown by the occurrence of fights for teats during suckling bouts at the sow's udder. Fights seemed to start when one animal retaliated against the other by biting it when its sucking behaviour caused discomfort. However, fights did not escalate into fierce battles because if one piglet started to walk away, another motivational state took over in its partner, resulting in suckling behaviour or even play behaviour. Also, a strong desire to rest in contact with the social partner seemed to allow tired piglets to put up with continual social harassment, rather than resulting in effective

retaliation or an attempt to escape by running away or jumping out of the cage. Therefore, early social isolation of piglets did not lead to abnormally high levels of aggression in the period following isolation.

Did recognition occur between incubator-reared piglets?

In the Pig Park, it was found that vigorous circle fighting, with biting, was more likely to occur in sow-reared piglets if they were unfamiliar. As the fights occurring between the incubator-reared piglets were interrupted by other types of behaviour, it may be that the piglets recognized each other after their limited experience together as littermates on the first day of life. However, this seems unlikely. Most of the piglets' energy on the day of birth was instinctively directed towards the vital task of finding and sucking colostrum from a teat. Information may have been gained incidentally on the smell of littermates, but Horrell (1982) found no evidence of a preference for littermates over non-littermates when piglets were tested in a T-maze between one and fourteen days of age. After separation for seventeen days, it is unlikely that the incubator-reared piglets would have been able to recognize each other by smell. Also, even if they were slightly familiar, they may still have fought to determine dominance. Recognition would have been more likely if the piglets had been separated for the same length of time at an older age (Ewbank and Meese, 1971).

Vocalizations

It has been reported that the levels of high-pitched vocalization were abnormally high in the incubators and flat-deck cages by comparison with the Pig Park. In the Pig Park, screaming was rare,

and was associated with unpleasant sensations such as pain when being crushed, fear when being handled and frustration when competing for a teat. Kiley (1972) also associated screaming with fear, isolation, pain and frustration. Whining was prolonged in the Pig Park when piglets were frustrated in their attempts to suckle because the sow was unwilling to suckle them. Kiley (1972) elicited this behaviour in situations of threat, fear, isolation, surprise, pain, frustration, anticipation and disturbance. Therefore, the high level of high-pitched vocalization occurring in the incubators and flat-deck cages was a good indication of a lack of well-being in these housing systems. Noyes (1976) obtained similar results in isolated gnotobiotic piglets, and related this to stress caused in the absence of the sow. Fraser (1975c) obtained increased levels of vocalization (grunts and squeals) when piglets were isolated for five minutes in an unfamiliar pen, and vocalization was reduced if placed in an unfamiliar pen with the sow and/or littermates (Fraser, 1975d). In the incubators and flat-decks, loud high-pitched vocalizations were associated with removal from the sow to a new environment and with frustration at feeding time (caused by blocked nipple drinkers, hearing other piglets being fed, etc.).

Welfare

It has been shown that many abnormalities of behaviour occurred in piglets reared in incubators and flat-deck cages, when compared with piglets raised in the Pig Park. Abnormalities were found not only in the greatly altered frequency and duration of many behaviour patterns, but also in their form and orientation. If the abnormal performance of a behaviour pattern satisfies the piglet's requirement

to perform that behaviour, then one could say that the piglet has been able to adapt to its environment in a satisfactory manner. However, the results suggest that some of the abnormal behaviour of the piglets in the incubators and flat-deck cages was indicative of a lack of well-being. For example, high levels of distress vocalization and the development of stereotypic behaviour indicate inadequacies in the environment, as does the redirection of common behaviour patterns towards inappropriate substrates.

The separation of piglets from their mothers long before the natural time of weaning has many consequences. It results in an increased risk of infection and of digestive disorders caused by a sudden change to a less appropriate diet. It also upsets a major part of the piglet's behavioural repertoire - its suckling behaviour. Many important stimuli which emanate from the sow and encourage the piglet to direct its suckling behaviour towards her udder are removed. Because suckling behaviour is normally so important for the survival of the piglet, a strong internal motivation to perform suckling behaviour must have arisen during evolution. When stimuli important for the release of suckling behaviour are absent, this motivation is frustrated (see Wood-Gush *et al.*, 1975; Stolba, 1981) and the behaviour becomes directed towards sub-optimal stimuli.

Keeping piglets in very barren and restricted environments also has detrimental effects on their well-being in that, apart from affecting their physical development, they are frustrated by the lack of space and suitable substrates for the performance of many behavioural sequences. Stereotyped behaviour develops when the piglet has become thoroughly habituated to all aspects of the barren

environment, and it then over-reacts when suddenly confronted with novel stimuli (Stolba and Wood-Gush, 1980). In a rich environment, there are endless sources of novelty to satisfy a piglet's exploratory and play requirements, against a background of safety and comfort provided by the mother and other familiar aspects of the environment. In the barren flat-deck cages, manipulatory behaviour was redirected towards a pen-mate, probably as this was the most interesting object available, as the effect of manipulating it was, to some extent, unpredictable. Stolba (1981) also found that behaviour directed towards inanimate objects in the Pig Park became increasingly directed towards social companions as the environment became more barren. As with redirected suckling behaviour, this type of behaviour is undesirable.

No direct evidence was obtained which would indicate that permanent detrimental effects on social behaviour resulted from the rearing of piglets in social isolation between their second and eighteenth day of life. This is because the effects of social isolation were confounded by the effects of physical restriction, ill health and a barren environment. In addition, when removed from social isolation, the piglets were given only one social companion, and they were not observed as adults.

Social isolation did affect the piglets while in the incubators by depriving them of the chance to control their body temperature by means of huddling with other pigs. The deaths of four piglets after a heating failure may have been prevented if social contact had been possible. The observation that the piglets almost always rested in contact with each other after introduction to the flat-decks suggest that they may have suffered from a denial of the

opportunity to control their temperature by behavioural means.

Social interaction with a variety of pigs of different sexes, ages, degrees of aggressiveness, degrees of willingness to play, etc., is important if a piglet is to learn how its behaviour affects the behaviour of others. It must learn the consequences of its behaviour upon different individual individuals in different contexts so that it can develop effective strategies for preventing injury to itself while gaining maximum benefit from proximity to, and interaction with, other pigs. While the piglets were in the incubators, they were unable to embark on this process of social learning. It is possible that they were able to make up for this quickly when transferred to the flat-deck cages, thereby not suffering permanent effects on their social behaviour. However, they only had one equally inexperienced piglet with which to gain social experience. Both incubator-reared and sow-reared piglets in the flat-decks showed higher levels of social interaction involving contact than the Pig Park piglets. In the Pig Park, much more subtle means of communication were possible, involving orientation towards and avoidance of others, without contact.

The ability to form and maintain close social bonds after early social isolation depends on the natural social behaviour of the species. Whereas rhesus monkeys isolated for their first nine months are hyperaggressive and sexually incompetent (Harlow and Harlow, 1969), pigtail monkeys, *Macaca nemestrina*, are able to form peer relationships and to accept strangers. The pigtail monkey normally forms less cohesive social groups than the rhesus monkey (Immelmann and Suomi, 1981). As pigs in the Pig Park form a stable social group and exclude strangers from the communal nest for months

after their introduction to the Pig Park (Stolba, 1982), it is likely that early social isolation of piglets has a detrimental effect on their social behaviour.

If the incubator-reared piglets had been transferred into a group of socially-reared piglets, they would probably have been less able to compete for limited resources because they lacked social experience and were weaker as a result of lack of exercise in the incubators. Also, their desire to massage and suck the other piglets' bodies may have resulted in severe retributions, which might not have prevented them from continuing to perform this ill-adapted behaviour. Therefore, it is likely that their social naiveté would have resulted in injury and poor growth rates.

The effects of early social isolation may not be evident at all times or in all environments. In Mongolian gerbils, *Meriones unguiculatus*, Ågren and Meyerson (1979) found that behavioural differences in aggression between controls and isolates disappeared after the isolates were housed with a cagemate, but when both isolates and controls were later isolated, the isolate group showed a more rapid increase in aggression. It would therefore be of interest to determine how incubator-reared piglets would react to future changes in their social and physical environment.

GENERAL CONCLUSIONS

The ancestors of the domestic pig evolved in a forest environment (Kiley, 1972), and piglet behaviour appears to retain many features adaptive for life in such an environment. Firstly, piglets remain in groups when active, which is presumably adaptive as an anti-predator mechanism through a number of possible means (increased vigilance, confusion of predators, increased ease of defence by adults, the 'selfish herd' effect). Piglets living in the wild are subjected to predation pressure from a variety of carnivorous species, depending on where they live. For example, bobcats, bears, alligators, and panthers are reported to prey on the piglets of feral swine in the south eastern United States (Hanson and Karstad, 1959).

Secondly, by huddling together while resting, piglets are able to keep warm in cool climates despite their small size, and this has probably been an important factor in their colonization of temperate regions. Other ungulates living at such latitudes do not show nesting behaviour and produce only one or two large-bodied young (Geist, 1981).

Thirdly, by becoming integrated into their mother's social group and staying with it, piglets presumably obtain the benefit of learning where to find clumped and ephemeral food supplies by following older knowledgeable animals. It is known that groups of wild pigs travel to different areas at different times of year in search of different crops (Kurz and Marchinton, 1972). Also, the finding that social facilitation occurred in piglets in the Pig Park demonstrates that they were aware of the activities of those around

them. This social awareness probably has local effects in guiding them to good rooting sites.

Therefore, despite the short period of their recent history in which the pressures of avoiding predators, locating nest sites and huddling with other group members for warmth, and locating and exploiting sources of milk, solid food and water, have been relaxed or removed by intensive farming, piglets still exhibit behavioural responses adaptive for life in the wild. Their behavioural repertoire has probably been little changed by domestication.

It is difficult to interpret the results obtained from the rearing of piglets in individual incubators because the effects of social isolation were confounded by ill health, confined conditions, a barren environment and additional stimuli obtained during efforts to keep the piglets alive. Concerning the latter, for example, the provision of medical care and the unblocking of nipple drinkers involved handling and other uncontrolled interactions with humans. Even if piglets were isolated in a more spacious, comfortable environment, and were provided with an opportunity to control environmental factors such as temperature by operant means, it would still be necessary to determine the effects on social behaviour of deprivation of the many different stimuli normally obtained in a social setting. It is often difficult to define the precise stimuli from which an individual is being isolated. Therefore, although comparisons made of the behaviour of incubator-reared and Pig Park-reared piglets indicate the range of behaviour appearing in socially barren and socially enriched conditions, they do not provide a clear demonstration of the effects of social isolation on later social behaviour. However, comparisons made between incubator-

reared and sow-reared piglets in flat-deck cages do suggest that the behaviour of piglets kept in the same environment becomes similar in many respects with time regardless of differing social histories.

SUGGESTIONS FOR FUTURE RESEARCH

It is evident that there are still large gaps in our knowledge of the social development and organization of pigs. A study of mother-infant relations, with reference to differences in maternal aggressiveness and responsiveness, could provide interesting results. Experimental work needs to be done on the factors affecting inter-individual distances between piglets, and observations on pigs living in less restricted surroundings than the Pig Park, are needed to determine the dynamics of group formation and dispersal, especially of juveniles. Other topics of interest include the factors affecting the weaning process and the development of sexual behaviour in males and females. Finally, work is necessary on the long-term effects of early social experiences on the social behaviour and reproductive performance of adult pigs.

ACKNOWLEDGEMENTS

I am very grateful for the guidance and encouragement of my supervisor, Professor D.G.M. Wood-Gush, throughout this study.

Thanks must also go to Dr. V. Fowler, Dr. M. Varley and Miss A. Maitland for their great help and cooperation during my stay at the Rowett Institute.

I would like to thank Dr. A. Stolba for valuable discussions on methodology and Miss P. Phillips for statistical advice.

I am grateful for the technical assistance of the members of the Pig Unit staff at Easter Howgate, particularly that of M. Oliver and I. Agar, who were responsible for the health and welfare of the pigs in the Pig Park.

Thanks are due to G. Finnie for drawing Figures 1.24-1.27, 1.30-1.33 and 2.1.

Finally, I am indebted to Mrs P. Gallie for the care and speed with which she has typed this thesis.

The work was funded by a Vans Dunlop Scholarship from the Faculty of Science at Edinburgh University.

REFERENCES

ALLISON, C.J. (1976) Snout-rubbing as a vice in weaned pigs. Vet. Rec. 98, 254-255.

ALTMANN, J. (1980) Baboon mothers and infants Harvard Univ. Press, London. 242 pp.

ARCHER, J. (1976) The organization of aggression and fear in vertebrates. In Perspectives in ethology Vol. 2, pp. 231-298. Eds. P.P.G. Bateson and P.H. Klopfer, Plenum Press, New York.

ÅRGREN, G. and MEYERSON, B.J. (1979) Long term effects of social deprivation during early adulthood in the Mongolian gerbil *(Meriones unguiculatus)*. Z. Tierpsychol. 47, 422-431.

ASH, R.W. and HEAP, R.B. (1975) Oestrogen, progesterone and corticosteroid concentrations in peripheral plasma of sows during pregnancy, parturition, lactation and after weaning. J. Endocr. 64, 141-154.

BALDWIN, J.D. (1969) The ontogeny of social behaviour of Squirrel monkeys *(Saimiri sciureus)* in a seminatural environment. Folia primatol. 11, 35-79.

BALDWIN, J.D. and BALDWIN, J.I. (1974) Exploration and social play in Squirrel monkeys *(Saimiri)*. Am. Zool. 14, 303-315.

BARBER, R.S., BRAUDE, R. and MITCHELL, K.G. (1955) Studies on milk production of Large White pigs. J. agric. Sci., Camb. 46, 97-118.

BATESON, P.P.G. (1976) Rules and reciprocity in behavioral development. In Growing points in ethology pp. 401-421. Eds. P.P.G. Bateson and R.A. Hinde, Cambridge Univ. Press, Cambridge.

BATESON, P.P.G. (1981) Discontinuities in development and changes in the organization of play in cats. In Behavioral development, pp. 281-295. Eds. K. Immelmann, G.W. Barlow, L. Petrinovich and M. Main, Cambridge Univ. Press, Cambridge.

BEILHARZ, R.G. and COX, D.F. (1967) Social dominance in swine. Anim. Behav. 15, 117-122.

BEKOFF, M. (1974) Social play and play-soliciting by infant canids. Am. Zool. 14, 323-340.

BEKOFF, M. and BYERS, J.A. (1981) A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: An ethological hornet's nest. In Behavioral Development pp. 296-337. Eds. K. Immelmann, G.W. Barlow, L. Petrinovich and M. Main, Cambridge Univ. Press, Cambridge.

BERGER, J. (1979) Social ontogeny and behavioural diversity: Consequences for Bighorn sheep *Ovis canadensis*. J. Zool. 188, 251-266.

BERNSTEIN, I.S. (1970) Primate status hierarchies. In Primate behavior Vol. 1, pp. 71-109. Ed. L.A. Rosenblum, Academic Press, New York.

BERTRAM, B.C.R. (1976) Kin selection in lions and in evolution. In Growing points in ethology pp. 281-301. Eds. P.P.G. Bateson and R.A. Hinde, Cambridge Univ. Press, Cambridge.

BEUERLE, W. (1975) Field observations on the aggressive and sexual behaviour of the European wild hog. Z. Tierpsychol. 39, 211-258.

BIBEN, M. (1982) Sex differences in the play of young ferrets. Biol. Behav. 4, 303-308.

BLACKSHAW, J.K. (1980) Environmental design and the responses of weaned pigs. In Behaviour: Reviews in Rural Science IV, 143-145. Eds. M. Wodzicka-Tomaszewska, T.N. Edey and J.J. Lynch, The University of New England, Armidale.

BOOTH, W.D. (1982) Testicular steroids and boar taint. In Control of pig reproduction, pp. 25-48. Eds. D.J.A. Cole and G.R. Foxcroft, Butterworths Scientific, London.

BROWNLEE, A. (1954) Play in domestic cattle in Britain: an analysis of its nature. Br. vet. J. 110, 48-68.

CAMPBELL, R.G. and DUNKIN, A.C. (1982) The effect of birth weight on the estimated milk intake, growth and body composition of sow-reared piglets. Anim. Prod. 35, 193-197.

CHALMERS, N.R. and LOCKE-HAYDON, J. (1981) Temporal patterns of play bouts in captive common marmosets *(Callithrix jacchus)* Anim. Behav. 29, 1229-1238.

CHEPKO, B.D. (1971) A preliminary study of the effects of play deprivation on young goats. Z. Tierpsychol. 28, 516-526.

CLARKE, R.S., HERON, W., FETHERSTONHAUGH, M.L., FORGAYS, D.G. and HEBB, D.O. (1951) Individual differences in dogs: preliminary report on the effects of early experience. Can. J. Psychol. 5, 150-156.

COLENBRANDER, B., FRANKENHUIS, M.T. and WENSING, C.J.G. (1982) Male sexual development. In Control of pig reproduction, pp. 3-24. Eds. D.J.A. Cole and G.R. Foxcroft, Butterworths Scientific, London.

DAWKINS, R. (1976) The selfish gene, pp. 224. Oxford Univ. Press, Oxford.

EIBL-EIBESFELDT, I. (1967) Concepts of ethology and their significance in the study of human behavior. In Early behavior: comparative and developmental approaches, pp. 127-146. Eds. H. Stevenson, E. Hess and H. Rheingold, Wiley, New York.

ELSAESSER, F. (1982) Endocrine control of sexual maturation in the female pig and sexual differentiation of the stimulatory oestrogen feedback mechanism. In Control of pig reproduction pp. 93-116. Eds. D.J.A. Cole and G.R. Foxcroft, Butterworths Scientific, London.

EMORY, G.R. (1976) Attention structure as a determinant of social organization in the mandrill *(Mandrillus sphinx)* and the gelada baboon *(Theropithecus gelada)*. In The social structure of attention, pp. 29-49. Eds. M.R.A. Chance and R.R. Larsen, J. Wiley and Sons, London.

ENGLISH, P. (1982) Pig welfare into practice. Proceedings: Perth pig conference, pp. 25-34. Edinburgh School of Agriculture, Edinburgh.

EWBANK, R. and BRYANT, M.J. (1972) Aggressive behaviour amongst groups of domesticated pigs kept at various stocking rates. Anim. Behav. 20, 21-28.

EWBANK, R. and MEESE, G.B. (1971) Aggressive behaviour in groups of domestic pigs on removal and return of individuals. Anim. Prod. 13, 685-694.

EWBANK, R., MEESE, G.B. and COX, J.E. (1974) Individual recognition and the dominance hierarchy in the domestic pig. The rôle of sight. Anim. Behav. 22, 473-480.

FAGEN, R. (1976) Exercise, play and physical training in animals.

In Perspectives in Ethology 2, pp. 189-219. Eds. P.P.G. Bateson and P.H. Klopfer, Plenum Press, London.

FENTRESS, J.C. (1981) Order in ontogeny: relational dynamics. In Behavioral development, pp. 338-371. Eds. K. Immelmann, G.W. Barlow, L. Petrinovich and M. Main, Cambridge Univ. Press, Cambridge.

FOWLER, V.R. and VARLEY, M.A. (1980) Recent developments in weaning at birth. Proc. Pig Vet. Soc., 7, 38-42.

FOX, M.W. and CLARK, A.L. (1971) The development and temporal sequencing of agonistic behavior in the coyote *(Canis latrans)*. Z. Tierpsychol. 28, 262-278.

FRÄDICH, H. (1974) A comparison of behaviour in the Suidae. In The behaviour of ungulates and its relation to management. Vol.1, pp. 133-143. Eds. V. Geist and F. Walther. International Union for the Conservation of Nature and Natural Resources, Morges, Switzerland.

FRASER, D. (1973) The nursing and suckling behaviour of pigs. I. The importance of stimulation of the anterior teats. Br. vet. J. 129, 324-336.

FRASER, D. (1974) The behaviour of growing pigs during experimental social encounters. J. agric. Sci., Camb. 82, 147-163.

FRASER, D. (1975a) The nursing and suckling behaviour of pigs. IV. The effect of interrupting the suckling stimulus. Br. vet. J. 131, 549-559.

FRASER, D. (1975b) The 'teat order' of suckling pigs. II. Fighting during suckling and the effects of clipping the eye teeth. J. agric. Sci., Camb. 84, 393-399.

FRASER, D. (1975c) Vocalizations of isolated piglets. I. Sources of variation and relationships among measures. Appl. Anim. Ethol. 1, 387-394.

FRASER, D. (1975d) Vocalizations of isolated piglets. II. Some environmental factors. Appl. Anim. Ethol. 2, 19-24.

FRASER, D. (1977) Some aspects of milk ejection failure by sows. Br. vet. J. 133, 126-133.

FRASER, D. (1978) Observations on the behavioural development of suckling and early-weaned piglets during the first six weeks after birth. Anim. Behav. 26, 22-30.

FRASER, D. and MORLEY-JONES, R. (1975) The 'teat order' of suckling pigs. I. Relation to birth weight and subsequent growth. J. agric. Sci., Camb. 84, 387-391.

FRASER, D., THOMSON, B.K., FERGUSON, D.K. and DARROCH, R.L. (1979) The 'teat order' of suckling pigs. 3. Relation to competition within litters. J. agric. Sci., Camb. 92, 257-261.

GEIST, V. (1971) Mountain sheep: a study in behaviour and evolution, 384 pp. Univ. of Chicago Press, Chicago.

GEIST, V. (1981) On the reproductive strategies in ungulates and some problems of adaptation. In Evolution today, pp. 111-132. Eds. G.G.E. Scudder and J.L. Reveal. Proc. 2nd Int. Congr. on Systematic and Evolutionary Biology.

GILL, J.C. and THOMSON, W. (1956) Observations on the behaviour of suckling pigs. Br. J. Anim. Behav. 4, 46-51.

GOLANI, I. (1976) Homeostatic motor processes in mammalian interactions: A choreography of display. In Perspectives in Ethology, Vol. 2, pp. 69-134. Eds. P.P.G. Bateson and P.H. Klopfer, Plenum Press, London.

GUBERNICK, D.J. (1981) Parent and infant attachment in mammals. In Parental care in mammals, pp. 243-305. Eds. D.J. Gibernick

and P.H. Klopfer, Plenum Press, London.

HANSON, R.P. and KARSTAD, L. (1959) Feral swine in the South-eastern United States. J. Wildl. Mgmt. 23, 64-74.

HARLOW, H.F. and HARLOW, M.K. (1969) Effects of various mother-infant relationships on rhesus monkey behaviors. In Determinants of infant behavior, IV, pp. 15-36. Ed. B.M. Foss, Methuen, London.

HARPER, L.V. (1981) Offspring effects upon parents. In Parental care in mammals, pp. 117-177. Eds. D.J. Gubernick and P.H. Klopfer, Plenum Press, London.

HARTSOCK, T.G., GRAVES, H.B. and BAUMGARDT, B.R. (1977) Agonistic behavior and the nursing order in suckling piglets: Relationships with survival, growth and body composition. J. Anim. Sci. 44, 320-330.

HEMSWORTH, P.H. (1982) Social environment and reproduction. In Control of pig reproduction, pp. 585-601. Eds. D.J.A. Cole and G.R. Foxcroft, Butterworths Scientific, London.

HEMSWORTH, P.H., BEILHARZ, R.G. and GALLOWAY, D.B. (1977) Influence of social conditions during rearing on the sexual behaviour of the domestic boar. Anim. Prod. 24, 245-251.

HEMSWORTH, P.H., WINFIELD, C.G. and MULLANEY, P.D. (1976) A study of the development of the teat order in piglets. Appl. Anim. Ethol. 2, 225-233.

HINDE, R.A. (1970) Animal behaviour - a synthesis of ethology and comparative psychology, 876 pp. McGraw-Hill Book Co., New York.

HINDE, R.A. (1971) Some problems in the study of the development of social behaviour. In The biopsychology of development, pp. 411-432. Eds. E. Tobach, L.R. Aronson and E. Shaw, Academic Press, New York.

HINDE, R.A., ROWELL, T.E. and SPENCER-BOOTH, Y. (1964) Behaviour of socially living rhesus monkeys in their first six months. Proc. zool. Soc., Lond. 143, 609-649.

HODGSON, R.E. (1935) An eight-generation experiment in inbreeding swine. J. Hered. 26, 209-217.

HOLNESS, D.H. and HUNTER, R.H.F. (1975) *Post partum* oestrus in the sow in relation to the concentration of plasma oestrogens. J. Reprod. Fert. 45, 15-20.

HOLUB, A., FORMAN, Z. and JIZKOVA, D. (1957) Development of chemical thermoregulation in piglets. Nature, 180, 858-859.

HORRELL, I. (1982) Social interactions amongst fostered piglets. Appl. Anim. Ethol. 9, 86-87 (Abstr.).

HORRELL, I. and BENNETT, J. (1981) Disruption of teat preferences and retardation of growth following cross-fostering of 1-week old pigs. Anim. Prod. 33, 99-106.

HUTTON, R.C. (1979) Social facilitation as a measure of individual relationships in a pig group *(Sus. scrofa L)*. Unpublished Honours thesis, Department of Zoology, University of Edinburgh, Scotland. 45pp.

IMMELMANN, K. and SUOMI, S.J. (1981) Sensitive phases in development. In Behavioral development, 395-431. Eds. K. Immelmann, G.W. Barlow, L. Petrinovich and M. Main, Cambridge Univ. Press, Cambridge.

JARDINE, N. and SIBSON, R. (1968) The construction of hierarchic and non-hierarchic classifications. Comput. J. 11, 177-184.

JENSEN, P. (1982) An analysis of agonistic interaction patterns in group-housed dry sows - aggression regulation through an 'avoidance order'. Appl. Anim. Ethol. 9, 47-61.

JENSEN, P. and WOOD-GUSH, D.G.M. Social interactions in a group of free-ranging sows. Appl. Anim, Ethol. (In press).

JEPPESEN, L.E. (1980) The behaviour of piglets reared on an artificial sow. Unpublished PhD thesis, University of Cambridge, England.

KILEY, M. (1972) The vocalizations of ungulates, their causation and function. Z. Tierpsychol. 31, 171-222.

KUIPERS, M. and WHATSON, T.S. (1979) Sleep in piglets: an observational study. Appl. Anim. Ethol. 5, 145-151.

KUMMER, H. (1971) Primate societies, 160 pp. Aldine-Atherton Inc., Chicago.

KURZ, J.C. and MARCHINTON, R.L. (1972) Radiotelemetry studies of feral hogs in South Carolina. J. Wildl. Mgmt. 36, 1240-1248.

LAZAR, J.W. (1974) Social play or the development of social behavior in ferrets *(Mustela putorius)*. Am. Zool. 14, 405-414.

LECCE, J.G. (1969) Rearing colostrum-free pigs in an automated feeding device. J. Anim. Sci. 28, 27-33.

LECCE, J.G. (1971) Rearing neonatal piglets of low birth weight with an automatic feeding device. J. Anim. Sci. 33, 47-51.

LENT, P.C. (1974) Mother-infant relationships in ungulates. In The behaviour of ungulates and its relation to management Vol. 1, pp. 14-55. Eds. V. Geist and F. Walther, I.U.C.N., Morges, Switzerland.

LIEN, J. and KLOPFER, F.D. (1978) Some relations between stereotyped suckling in piglets and exploratory behavior and discrimination reversal learning in adult swine. Appl. Anim. Ethol. 4, 223-234.

LOIZOS, C. (1966) Play in mammals. Symp. zool. Soc., Lond. 18, 1-9.

LORENZ, K.Z. (1981) The foundations of ethology, 380 pp. Springer-Verlag, New York.

MAUGET, R. (1982) Seasonality of reproduction in the wild boar. In Control of pig reproduction, pp. 509-526. Eds. D.J.A. Cole and G.R. Foxcroft, Butterworths Scientific, London.

McBRIDE, G. (1963) The 'teat order' and communication in young pigs. Anim. Behav. 11, 53-56.

McBRIDE, G., JAMES, J.W. and HODGENS, N. (1964) Social behaviour of domestic animals. IV. Growing pigs. Anim. Prod. 6, 129-139.

McBRIDE, G., JAMES, J.W. and WYETH, G.S.F. (1965) Social behaviour of domestic animals. VII. Variation in weaning weight in pigs. Anim. Prod. 7, 67-74.

MEESE, G.B. and BALDWIN, B.A. (1975) Effects of olfactory bulb ablation on maternal behaviour in sows. Appl. Anim. Ethol. 1, 379-386.

MEESE, G.B. and EWBANK, R. (1972) A note on instability of the dominance hierarchy and variations in level of aggression within groups of fattening pigs. Anim. Prod. 14, 359-362.

MEESE, G.B. and EWBANK, R. (1973a) The establishment and nature of the dominance hierarchy in the domestic pig. Anim. Behav. 21, 326-334.

MEESE, G.B. and EWBANK, R. (1973b) Exploratory behaviour and leadership in the domestic pig. Br. vet. J. 129, 251-259.
MORGAN, B.J.T., SIMPSON, M.J.A., HANBY, J.P. and HALL-CRAGGS, J. (1976) Visualizing interaction and sequential data in animal behaviour: Theory and application of cluster analysis methods. Behaviour, 56, 1-43.
MORRIS, D. (1964) The response of animals to a restricted environment. Symp. zool. Soc., Lond. 13, 99-118.
MOUNT, L.E. (1968) The climatic physiology of the pig, 271 pp. Edward Arnold, London.
MÜLLER-SCHWARZE, D. (1968) Play deprivation in deer. Behaviour 31, 144-162.
NOYES, L. (1976) A behavioural comparison of gnotobiotic with normal neonate pigs, indicating stress in the former. Appl. Anim. Ethol. 2, 113-121.
OWENS, N.W. (1972) The development of behaviour in free-living baboons *(Papio anubis)*. Unpublished PhD thesis, University of Cambridge, England. 176 pp.
PITTAWAY, M.J. and BROWN, P.L. (1974) Early weaning and cage rearing: R.S.P.C.A. Report. Pig Fmg. 22(4), 26-29.
POIRIER, F.E. and SMITH, E.O. (1974) Socializing functions of primate play. Am. Zool. 14, 275-287.
POND, W.G. and HOUPT, K.A. (1978) The biology of the pig, 371 pp. Cornell University Press, Ithaca.
POOLE, T.B. (1966) Aggressive play in polecats. Symp. zool. Soc. Lond., 18, 23-44.
PROHÁSKA, L. (1981) Studies on the predisposing rôle of stress in the *E. coli*- diarrhoea of pigs. Vet. Bull, Weybridge, 51, 514. (Abstr.).
RASA, O.A.E. (1971) Social interaction and object manipulation in weaned pups of the northern elephant seal *(Mirounga angustirostris)*. Z. Tierpsychol. 29, 82-102.
RASMUSSEN, O.G., BANKS, E.M., BERRY, T.H. and BECKER, D.E. (1962) Social dominance in gilts. J. Anim. Sci. 21, 520-522.
RHEINHARDT, V. and RHEINHARDT, A. (1982) Social behaviour and social bonds between juvenile and sub-adult *Bos indicus* calves. Appl. Anim. Ethol. 9, 92-93. (Abstr.).
RILEY, V. (1981) Psychoneuroendocrine influences on immunocompetence and neoplasia. Science, 212, 1100-1109.
ROSENBLATT, J.S. and SIEGEL, H.I. (1981) Factors governing the onset and maintenance of maternal behavior among nonprimate mammals. The rôle of hormonal and nonhormonal factors. In Parental care in mammals, 13-76. Eds. D.J. Gubernick and P.H. Klopfer, Plenum Press, London.
ROWELL, T.E. (1974) The concept of social dominance. Behav. Biol. 11, 131-154.
SAMBRAUS, H.H. (1981) Abnormal behavior as an indication of immaterial suffering. Int. J. Stud. Anim. Probl. 2, 245-248.
SAYLOR, A. and SALMON, M. (1971) An ethological analysis of communal nursing by the house mouse *(Mus musculus)*. Behaviour 40, 62-85.
SCHEEL, D.E., GRAVES, H.B. and SHERRITT, G.W. (1977) Nursing order, social dominance and growth in swine. J. Anim. Sci. 45, 219-229.
SCOTT, J.P. and MARSTON, M.V. (1950) Social facilitation and

allelomimetic behaviour in dogs. II. The effects of unfamiliarity. Behaviour, 2, 135-143.

SIEGEL, S. (1956) Nonparametric statistics for the behavioural sciences, 312 pp. McGraw-Hill Kogokusha Ltd., London.

SIGNORET, J.P., BALDWIN, B.A., FRASER, D. and HAFEZ, E.S.E. (1975) The behaviour of swine. In Behaviour of domestic animals. 295-329. Ed. E.S.E. Hafez, Ballière Tindall, London.

SIMMEL, E.C. and BAKER, E. (1980) The effects of early experiences on later behavior: A critical discussion. In Early experiences and early behavior - implications for social development, pp. 4-13. Ed. E.C. Simmel, Academic Press, London.

SLATER, P.J.B. and OLLASON, J.C. (1972) The temporal pattern of behaviour in isolated male zebra finches: Transition analysis. Behaviour, 42, 248-268.

SMITH, E.O. (1978) A historical view on the study of play - Statement of the problem. In Social play in primates, pp. 1-32. Ed. E.O. Smith, Academic Press, New York.

STEINER, A.L. (1971) Play activity of Columbian ground squirrels. Z. Tierpsychol. 28, 247-261.

STOLBA, A. (1979) Minimal ethological requirements for appropriate pig housing. Unpublished report, 39 pp. Edinburgh School of Agriculture, Edinburgh.

STOLBA, A. (1981) A family system in enriched pens as a novel method of pig housing. In Alternatives to intensive husbandry systems, pp. 52-67. The Universities Federation for Animal Welfare, Potters Bar, Hertfordshire.

STOLBA, A. (1982) Designing pig housing conditions according to patterns of social structure. Proceedings: Perth Pig Conference, Edinburgh School of Agriculture, Edinburgh. pp. 11-24.

STOLBA, A. and WOOD-GUSH, D.G.M. (1980) Arousal and exploration in growing pigs in different environments. Appl. Anim. Ethol. 6, 382-383.

SVARE, B.B. (1981) Maternal aggression in mammals. In Parental care in mammals, pp. 179-210. Eds. D.J. Gubernick and P.H. Klopfer, Plenum Press, London.

THORPE, W.H. (1963) Learning and instinct in animals. Methuen and Co. Ltd., London. pp. 558.

TOLMAN, C.W. (1964) Social facilitation of feeding behaviour in the domestic chick. Anim. Behav. 12, 245-251.

TYLER, S.J. (1972) The behaviour and social organization of the New Forest ponies. Anim. Behav. Monogr. 5, 87-198.

VARLEY, M.A. (1982) The time of weaning and its effects on reproductive function. In Control of pig reproduction, pp. 459-478. Eds. D.J.A. Cole and G.R. Foxcroft, Butterworths Scientific, London.

WEBSTER, J. and SAVILLE, C. (1981) Rearing of veal calves. In Alternatives to intensive husbandry systems, pp. 86-94. U.F.A.W., Potters Bar, Hertfordshire.

WELKER, W.I. (1971) Ontogeny of play and exploratory behaviors: A definition of problems and a search for new conceptual solutions. In The ontogeny of vertebrate behavior, 171-210. Ed. H. Moltz, Academic Press, New York.

WHATSON, T.S. (1979) Incomplete nursing in the sow. Appl. Anim. Ethol. 5, 195-196 (Abstr.).

WHATSON, T.S. and BERTRAM, J.M. (1983) Some observations on

mother-infant interactions in pigs (*Sus scrofa*). Appl. Anim. Ethol. 9, 253-262.

WILSON, E.O. 1975 Sociobiology: The new synthesis. 697 pp. Harvard Univ. Press, London.

WILSON, M.R. (1974) Immunological development of the neonatal pig. J. Anim. Sci. 38, 1018-1021.

WOOD-GUSH, D.G.M. (1983) Elements of ethology, 229 pp. Chapman and Hall, London.

WOOD-GUSH, D.G.M., DUNCAN, I.J.H. and FRASER, D. (1975) Social stress and welfare problems in agricultural animals. In The behaviour of domestic animals, pp. 182-200. Ed. E.S.E. Hafez, Bailliere Tindall, London.

WORSAAE, H. and SCHMIDT, M. (1980) Plasma cortisol and behaviour in early-weaned piglets. Acta. vet. scand. 21, 640-657.

Appendix A Temperature, rainfall and wind in the Pig Park during 1980

Month	Temperature (^{o}C)			Rainfall (mm)		No. of days with strong to gale force winds
	Mean Temp. at 1100 hours	Maximum Monthly temp.	Minimum Monthly temp.	Monthly total	Maximum in 1 day	
January	- 4.6	4	- 13	57	10	1
February	- 1.0	15	- 12	33	5	0
March	0.8	17.5	- 16	62	10	1
April	11.3	25.5	- 4	12	3	2
May	13.1	34	0	15	5	0
June	14.7	34	0	77	21	3
July	14.3	33.5	3.5	61	13	1
August	15.0	30.5	2	85	15	5
September	13.2	28.5	4	49	8	2
October	7.6	19	- 2.5	84	15	2
November	6.4	14	- 4	78	11	2

Appendix B1 ETHOGRAM OF PIGLET BEHAVIOUR PATTERNS OBSERVED IN THE PIG PARK

NO.	BEHAVIOUR PATTERN	DESCRIPTION
	Positions	
1	lie apart on belly	legs tucked under body or stretched forwards or backwards, no physical contact with other pigs
2	lie apart on side	legs stretched out to side
3	sit apart	sit on one or both haunches, forelegs support forequarters off ground
4	kneel apart	forelegs bent at knees, hindlegs upright
5	stand apart	stand on four feet, out of physical contact with other pigs, head may be up, neutral or hanging
6	alert stance	'freeze' in tense upright or crouched position, ears upright
	Locomotion	
7	walk	forward progression by movement of near-fore → off-hind → off-fore → near-hind; head neutral
8	step	move one step forward and pause to perform another behaviour, step around to face in different direction, step backwards
9	trot	forward progression by movement of off-hind together with near-fore followed by near-hind with off-fore
10	gallop	very rapid forward progression with long strides, head and body low to ground and tail streaming behind
11	slip, fall	lose balance, stumble, slip or fall to ground
12	crawl on belly	move about with belly in contact with ground
13	climb	step up on to raised object, place forefeet up against vertical object
	Play markers	
14	scamper	run with vertical and horizontal bouncy movements, direction of movement may form zig-zag path
15	hop	jump up and down once on spot
16	pivot	jump, whirl around to face in different direction

17	toss head	vigorous latero-rotationary movements of the head and neck
18	flop on belly, side	rapid but relaxed drop from upright to reclining position
19	bump*	bump into another piglet with head or body as if by accident
20	shake object	similar to 'toss head' but with object held in mouth
	Vocalizations	
21	slow grunting	short low-pitched grunts, may be repeated at intervals greater than or equal to one second, maintain auditory contact with group members during locomotion and foraging
22	rapid grunting	short low-to higher-pitched grunts repeated at intervals of less than one second, given during locomotion, especially if getting left behind, and during social greeting after period of separation
23	quack	rapidly repeated, open-mouthed, nasal-sounding vocalizations given during approach towards and naso-nasal contacts with adult group members, especially the mother sow
24	whine	long high-pitched vocalizations given prior to suckling and during attempts to suckle
25	squeak	short to long very high-pitched squeaks and twitters given by young piglets during activity, mainly in suckling context
26	squeal	short high-pitched sound given after receiving threat or bites from another pig, sign of submission
27	scream	long, loud, high-pitched, open-mouthed vocalization given when fighting for a teat or when being handled by man or crushed by an adult pig
28	bark	short, low-pitched, open-mouthed grunt given during rapid exhalation when alarmed by sudden external stimulus
29	threatening grunt*	short to long low-pitched exhalation grunt directed towards another pig when disturbed by it, especially during formation of a resting huddle and when feeding on food pellets, often associated with a 'knock'

	Comfort behaviour	
30	wag tail	lateral movements of tail performed to relieve irritation (from flies, after elimination, etc.) and during locomotion and play
31	yawn	stretching open of jaws with long inhalation, given mainly after waking up
32	cough, sneeze, loud 'sniff'	exhalations to clear nasal passage and throat
33	stretch	legs, trunk and/or head stretched out and then relaxed, usually occurs during or after rest period
34	headshake	small, rapid lateral movements of head given to relieve irritation (from flies, ear tags, etc.), also performed after physical contact with other pigs (e.g. after 'circling') maybe as a displacement activity, sometimes socially facilitated
35	scratch	use fore- or hindfoot to scratch belly, legs or head region
36	rub head	performed against objects as a comfort behaviour (in adults, may form part of 'marking' behaviour)
37	rub body	rub side of body up and down against object, squat and rub hind region back and forth along ground (especially after defecation), may be socially facilitated
38	urinate	females squat, males stand upright
39	defecate	both sexes may squat, especially during first week and when scouring, otherwise stand upright
	Investigative and feeding behaviour	
40	orient towards observer	approach within 1 metre and stretch nose towards observer
41	sniff, bite observer	sniff, nose and/or bite, mouth, pull, shake observer's clothing or skin
42	sniff ground	sniff, nose, chew at earth, grass and leaves, straw, food while upright or reclined
43	walk sniffing ground	walk forward slowly with head down sniffing along ground
44	sniff faeces	sniff, nose, mouth, eat faeces of pig
45	sniff urine	sniff, taste urine of pig on ground or while being eliminated
46	sniff object	sniff, nose rock, wood, metal, plastic,

		string, dead animal, solid (hard) vegetation, clump of sod, etc.
47	bite object	bite, mouth at above types of object
48	lever object	use snout to lift object off ground
49	tug, brace object	pull at object with mouth, hold down with fore foot
50	carry	move forward holding object, or mouthful of straw or grass which protrudes from side(s) of mouth
51	root	use snout disc to dig into earth with small, firm back-and-forth movements
52	shovel	use snout to lift and move forward loosened earth, straw, leaves, etc.
53	drink water	drink and nose water in stream, puddle, etc.
54	eat food	collect food pellets in mouth, chew and swallow
55	chew	make chewing movements while in upright or reclined position with head raised off ground
56	paw	stroke back-and-forth at earth, straw with fore-foot
	Social contact	
57	push past*	move past another pig making firm contact with side of body
58	climb on pig*	place forefeet or all four feet on back of a lying pig
59	lie contact on belly	as (1) but some part of body in physical contact with another pig
60	lie contact on side	as (2) but in contact
61	sit contact	as (3) but in contact
62	kneel contact	as (4) but in contact
63	stand contact	as (5) but in contact
	Agonistic behaviour (may be playful)	
64	knock*	rapid sideways movement of head towards another pig, usually aimed at head, usually hits other pig but does not always make contact
65	bite*	single or repeated snaps, slashes, bites with teeth, directed towards head and body of another pig, does not always make contact, may be vicious or inhibited
66	push heads, parallel*	mutual pushing, shoving or butting of sides of heads while facing in same

		direction
67	push heads, opposing*	as (66), but facing in opposite directions and may involve circling component
68	circle*	mutual pushing, shoving or butting at sides of body while circling around one another facing in opposite directions, lean in pressing shoulders and necks together
69	shove head*	use head to push at side of head of another pig (not mutual), heads may be lowered or raised
70	shove body*	use head and/or body to push at body of another pig (not mutual)
71	lever body*	use snout to lift fore- or hind-quarters of another pig off the ground
72	turn away*	lift head away from, turn whole body to face away from, walk or run away from within one metre of another pig
73	chase*	pursue another piglet as it moves rapidly away, usually associated with biting at flanks of retreating piglet
	Social investigation and manipulation	
74	orient towards*	approach within one metre of another pig, stretch nose towards it
75	sniff noses*	mutual contact of snout discs (usually with older animals) and mutual sniffing of heads
76	sniff head*	sniff, nose at head or ears of another pig
77	sniff body*	sniff, nose at other parts of body of another pig
78	chew head*	chew, suck or mouth at head or ears
79	chew body*	chew, suck or mouth at other parts of body, especially legs, joints, tail, hair bristles
	Elements of adult sexual behaviour	
80	anogenital sniff*	sniff, nose at anogenital region
81	attempted mount*	press chin on back of another piglet, may lift forelegs off ground
82	mount side*	place forefeet and/or belly on back or head of another upright piglet, incorrect orientation of body
83	mount rear*	mount another upright piglet from rear, i.e., correct orientation

Suckling behaviour

84	sniff udder	sniff, nose along udder of sow
85	suck teat	includes nosing, sucking, massaging and holding of teat. Massaging involves up-and-down rubbing of snout disc against the udder in the area around the teat
86	drink milk	rapid sucking and swallowing of milk during milk let-down
87	switch teats	rapid movements of head back and forth between two or more different teats
88	push for unexposed teat	push nose down under sow's belly in attempt to suck at unexposed teat (unexposed because sow lying on belly)
89	orient towards udder	stretch nose up towards teat while both sow and piglet upright
90	fight for teat*	push vigorously and bite at head of piglet holding desired teat (which pushes back with its head)
91	receive threat from sow	sow growls, stares, lunges at, or snaps at piglet, usually when weaning piglets
92	sniff udder of another sow	sniff, nose, suck, massage, hold teats of a sow other than piglet's own mother. If piglet started to suckle regularly from another sow and no longer from its own mother, the other sow was then considered to be its own (new) mother

* These behaviour patterns involve another pig, and, with the exception of the mutual behaviour patterns (66), (67), (68) and (75), could be both given or received at different times. Giving and receiving were distinguished along with the identities of the participants.

Appendix B.2 Behavioural frequencies of piglets in the Pig Park

Behaviour pattern		(A) mean frequency (times/30 min), (B) range (times/30 min), (C) mean no. 30 sec. intervals/30 min. and (D) range (intervals/30 min.) during each age period (days)						
		1-8	9-17	18-27	28-41	42-55	56-69	70-91
lie apart on belly	A	0.00	0.53	0.25	0.48	0.02	0.08	0.59
	B	-	0-11	0-4	0-5	0-1	0-1	0-9
	C	0.00	0.47	0.22	0.35	0.02	0.08	0.65
	D	-	0-10	0-4	0-3	0-1	0-1	0-8
lie apart on side		0.00	0.06	0.00	0.03	0.00	0.08	0.00
		-	0-2	-	0-1	-	0-1	-
		0.00	0.06	0.00	0.03	0.00	0.08	0.00
		-	0-2	-	0-1	-	0-1	-
sit apart		0.37	1.13	0.41	0.28	0.07	0.00	0.12
		0-4	0-12	0-4	0-3	0-1	-	0-2
		0.34	1.03	0.38	0.25	0.07	0.00	0.09
		0-3	0-10	0-3	0-3	0-1	-	0-1
kneel apart		0.00	1.31	1.00	0.45	0.04	0.08	0.74
		-	0-28	0-26	0-5	0-1	0-1	0-6
		0.00	0.78	0.81	0.43	0.04	0.08	0.71
		-	0-12	0-20	0-5	0-1	0-1	0-6
stand apart		6.61	14.34	10.47	10.43	8.89	11.23	10.65
		0-40	0-49	0-50	0-31	0-43	0-29	0-31
		5.46	11.94	8.31	9.03	7.87	8.77	9.06
		0-45	0-30	0-33	0-36	0-27	0-20	0-21
alert stance		0.26	0.66	1.81	0.83	0.33	0.77	0.59
		0-3	0-3	0-16	0-6	0-4	0-4	0-5
		0.24	0.66	1.75	0.81	0.28	0.77	0.59
		0-3	0-3	0-13	0-6	0-2	0-4	0-5
walk		20.00	36.47	30.66	37.88	35.78	45.85	47.44
		0-116	1-110	0-62	0-82	0-93	2-76	0-83
		12.79	24.50	22.19	26.05	23.94	27.77	30.50
		0-51	1-48	0-41	0-47	0-48	2-43	0-47
step		8.84	15.31	12.06	19.00	21.41	26.39	31.44
		0-52	1-44	0-46	0-46	0-54	0-44	1-57
		6.97	12.19	9.63	14.38	15.93	19.00	23.12
		0-37	1-29	0-29	0-31	0-37	0-31	1-36
trot		0.58	2.56	5.63	6.38	3.30	3.77	2.29
		0-8	0-16	0-29	0-36	0-15	0-9	0-11
		0.53	2.22	4.38	5.18	2.70	3.00	2.00
		0-7	0-13	0-19	0-24	0-14	0-6	0-9
gallop		0.29	1.34	4.22	1.65	0.50	0.54	0.44
		0-4	0-6	0-20	0-10	0-4	0-2	0-3
		0.29	1.53	3.88	1.58	0.50	0.54	0.41
		0-4	0-14	0-17	0-8	0-4	0-2	0-3
slip, fall		0.24	0.09	0.19	0.10	0.00	0.00	0.00
		0-3	0-3	0-2	0-2	-	-	-
		0.24	0.09	0.19	0.10	0.00	0.00	0.00
		0-2	0-3	0-2	0-2	-	-	-
crawl on belly		0.29	0.19	0.31	0.30	0.28	0.08	0.18
		0-3	0-3	0-7	0-4	0-4	0-1	0-3
		0.24	0.19	0.16	0.30	0.26	0.08	0.18
		0-2	0-3	0-2	0-4	0-4	0-1	0-3

Appendix B.2 (continued)

Behaviour pattern	1-8	9-17	18-27	28-41	42-55	56-69	70-91
climb	0.26	0.09	0.00	0.18	0.44	1.31	0.38
	0-2	0-1	-	0-2	0-9	0-6	0-3
	0.26	0.09	0.00	0.18	0.41	1.15	0.38
	0-2	0-1	-	0-2	0-8	0-6	0-3
scamper	1.24	5.81	9.47	6.88	2.44	3.23	2.21
	0-12	0-24	0-34	0-25	0-19	0-11	0-15
	0.95	5.94	11.13	6.98	2.76	3.23	2.21
	0-9	0-22	0-41	0-27	0-22	0-12	0-11
hop	1.34	2.34	1.03	1.83	0.98	0.31	0.71
	0-9	0-10	0-4	0-7	0-14	0-1	0-3
	1.21	2.00	1.03	1.85	0.98	0.31	0.65
	0-6	0-8	0-4	0-5	0-11	0-1	0-3
pivot	0.45	1.34	2.19	2.05	0.85	1.15	0.68
	0-4	0-6	0-8	0-9	0-10	0-10	0-6
	0.42	1.34	2.09	1.80	0.76	0.77	0.68
	0-4	0-6	0-7	0-8	0-9	0-5	0-6
toss head	0.32	0.81	0.66	0.73	0.37	0.54	0.62
	0-2	0-6	0-3	0-6	0-3	0-3	0-5
	0.32	0.78	0.66	0.65	0.37	0.54	0.56
	0-2	0-5	0-3	0-5	0-6	0-3	0-5
flop on side, belly	0.00	0.06	0.00	0.00	0.00	0.15	0.03
	-	0-1	-	-	-	0-2	0-1
	0.00	0.06	0.00	0.00	0.00	0.15	0.03
	-	0-1	-	-	-	0-2	0-1
bump	0.16	0.44	0.50	0.18	0.22	0.13	0.44
	0-2	0-5	0-4	0-2	0-3	0-1	0-4
	0.16	0.41	0.50	0.18	0.22	0.13	0.38
	0-2	0-4	0-4	0-2	0-3	0-1	0-4
shake object	0.05	0.31	0.22	0.28	0.24	0.54	0.27
	0-2	0-5	0-1	0-4	0-9	0-3	0-2
	0.05	0.28	0.22	0.25	0.24	0.39	0.29
	0-2	0-5	0-1	0-3	0-6	0-2	0-3
slow grunting	4.90	13.28	10.31	12.48	11.76	23.23	9.97
	0-41	0-65	0-58	0-39	0-51	1-54	0-32
	3.66	10.03	7.47	9.60	8.41	19.31	8.18
	0-28	0-43	0-35	0-26	0-29	1-48	0-26
rapid grunting	3.97	4.50	4.84	3.98	2.33	6.62	1.77
	0-30	0-16	0-21	0-12	0-16	0-18	0-14
	4.55	3.94	4.19	3.53	2.13	5.62	1.62
	0-48	0-15	0-15	0-10	0-14	0-16	0-9
quack	0.32	0.44	0.13	0.03	0.07	0.00	0.00
	0-5	0-7	0-2	0-1	0-1	-	-
	0.29	0.31	0.09	0.03	0.07	0.00	0.00
	0-4	0-4	0-1	0-1	0-1	-	-
whine	0.71	1.13	0.97	0.75	1.39	2.08	0.71
	0-32	0-9	0-6	0-4	0-9	0-13	0-4
	0.82	1.03	0.84	0.70	1.24	1.77	0.68
	0-38	0-6	0-5	0-4	0-9	0-10	0-4
squeak	1.79	0.78	0.19	0.15	0.04	0.00	0.00
	0-15	0-4	0-1	0-2	0-2	-	-
	1.97	0.72	0.19	0.13	0.04	0.00	0.00
	0-21	0-3	0-1	0-1	0-2	-	-

Appendix B.2 (continued)

Behaviour pattern	1-8	9-17	18-27	28-41	42-55	56-69	70-91
squeal	0.11	0.41	0.41	0.60	0.70	0.54	0.65
	0-2	0-4	0-2	0-4	0-5	0-2	0-3
	0.11	0.31	0.38	0.60	0.65	0.54	0.65
	0-2	0-2	0-2	0-4	0-4	0-2	0-3
scream	0.03	0.00	0.00	0.00	0.04	0.00	0.00
	0-1	-	-	-	0-1	-	-
	0.03	0.00	0.00	0.00	0.04	0.00	0.00
	0-1	-	-	-	0-1	-	-
bark	0.00	0.03	0.09	0.08	0.09	0.23	0.27
	-	0-1	0-1	0-1	0-1	0-2	0-7
	0.00	0.03	0.09	0.08	0.09	0.23	0.27
	-	0-1	0-1	0-1	0-1	0-2	0-7
threatening grunt	0.00	0.03	0.00	0.20	0.09	0.31	1.27
	-	0-1	-	0-2	0-1	0-2	0-7
	0.00	0.03	0.00	0.20	0.09	0.23	1.21
	-	0-1	-	0-2	0-1	0-1	0-7
wag tail	0.29	2.19	2.75	6.18	4.22	7.46	8.94
	0-6	0-17	0-12	0-32	0-41	0-35	0-67
	0.21	1.91	2.50	5.18	3.24	5.62	6.88
	0-3	0-14	0-10	0-23	0-25	0-24	0-43
yawn	0.24	0.16	0.03	0.23	0.13	0.15	0.18
	0-1	0-2	0-1	0-6	0-1	0-1	0-2
	0.24	0.16	0.03	0.20	0.13	0.15	0.18
	0-1	0-2	0-1	0-5	0-1	0-1	0-2
cough, sneeze 'sniff'	0.13	0.06	0.09	0.63	1.44	2.23	1.82
	0-1	0-1	0-1	0-10	0-13	0-14	0-11
	0.13	0.06	0.09	0.55	1.33	1.77	1.62
	0-1	0-1	0-1	0-9	0-13	0-10	0-11
stretch	0.18	0.00	0.03	0.10	0.09	0.00	0.24
	0-2	-	0-1	0-2	0-1	-	0-4
	0.18	0.00	0.03	0.10	0.09	0.00	0.24
	0-2	-	0-1	0-2	0-1	-	0-4
headshake	2.05	1.44	1.34	1.53	1.65	3.00	2.74
	0-10	0-6	0-8	0-8	0-10	0-6	0-13
	1.84	1.31	1.25	1.40	1.54	2.92	2.68
	0-9	0-5	0-8	0-8	0-10	0-6	0-11
scratch	0.08	0.65	0.34	1.16	0.78	0.70	0.85
	0-1	0-3	0-3	0-6	0-10	0-4	0-4
	0.08	0.65	0.31	1.08	0.61	0.70	0.77
	0-1	0-3	0-2	0-6	0-6	0-4	0-4
rub head	0.05	0.16	0.06	0.30	0.11	0.15	0.41
	0-2	0-3	0-1	0-2	0-2	0-1	0-4
	0.05	0.16	0.06	0.30	0.11	0.15	0.41
	0-2	0-3	0-1	0-2	0-2	0-1	0-4
rub body	0.13	0.44	0.03	0.60	0.52	0.23	0.59
	0-3	0-8	0-1	0-5	0-7	0-3	0-5
	0.13	0.34	0.03	0.53	0.39	0.15	0.50
	0-3	0-6	0-1	0-5	0-4	0-2	0-4
urinate	0.24	0.50	0.16	0.30	0.33	0.46	0.65
	0-1	0-3	0-2	0-2	0-2	0-1	0-1
	0.24	0.44	0.13	0.23	0.33	0.46	0.65
	0-1	0-2	0-1	0-1	0-2	0-1	0-1

Appendix B.2 (continued)

Behaviour pattern	1-8	9-17	18-27	28-41	42-55	56-69	70-91
defecate	0.21	0.28	0.16	0.38	0.96	2.00	1.62
	0-3	0-4	0-2	0-3	0-4	0-8	0-8
	0.16	0.28	0.13	0.35	0.96	1.85	1.47
	0-3	0-4	0-1	0-3	0-4	0-8	0-6
orient towards observer	0.13	0.41	0.50	0.98	0.98	0.69	1.06
	0-2	0-2	0-3	0-5	0-6	0-3	0-5
	0.13	0.41	0.50	0.98	0.98	0.69	1.06
	0-2	0-2	0-3	0-5	0-6	0-3	0-5
sniff, bite observer	0.40	1.34	1.25	1.98	1.91	1.15	1.29
	0-8	0-12	0-5	0-9	0-10	0-4	0-4
	0.37	1.28	0.97	1.43	1.50	1.00	1.18
	0-7	0-9	0-4	0-7	0-6	0-3	0-4
sniff ground	8.97	25.38	21.63	28.75	30.67	41.85	44.32
	0-53	0-83	0-69	0-79	0-100	3-87	1-90
	7.68	19.13	16.28	19.93	23.80	28.39	31.38
	0-32	0-45	0-42	0-45	0-55	2-51	1-53
walk sniffing ground	0.24	2.06	2.34	3.18	3.46	5.54	6.29
	0-5	0-18	0-12	0-16	0-22	0-15	0-30
	0.24	2.03	2.25	2.98	3.38	5.08	5.85
	0-5	0-18	0-13	0-14	0-20	0-13	0-26
sniff faeces	0.08	0.31	0.03	0.10	0.11	0.08	0.03
	0-2	0-6	0-1	0-2	0-1	0-1	0-1
	0.08	0.28	0.03	0.08	0.11	0.08	0.03
	0-2	0-5	0-1	0-1	0-1	0-1	0-1
sniff urine	0.00	0.03	0.00	0.00	0.00	0.08	0.06
	-	0-1	-	-	-	0-1	0-1
	0.00	0.03	0.00	0.00	0.00	0.08	0.06
	-	0-1	-	-	-	0-1	0-1
sniff object	1.68	4.84	2.59	3.10	3.52	3.00	6.62
	0-12	0-18	0-11	0-10	0-18	0-10	0-35
	1.90	4.03	2.34	2.58	2.98	2.62	5.29
	0-11	0-13	0-9	0-8	0-13	0-10	0-25
bite object	0.66	2.16	2.13	2.38	2.57	1.39	6.06
	0-7	0-13	0-12	0-15	0-14	0-7	0-38
	0.61	2.06	1.94	2.15	2.57	1.08	5.41
	0-6	0-12	0-11	0-13	0-14	0-5	0-32
lever object	0.03	0.00	0.19	0.10	0.00	0.08	0.06
	0-1	-	0-2	0-2	-	0-1	0-1
	0.03	0.00	0.19	0.08	0.00	0.08	0.06
	0-1	-	0-2	0-1	-	0-1	0-1
tug, brace object	0.00	0.34	0.38	0.25	0.24	0.62	0.59
	-	0-2	0-3	0-3	0-4	0-4	0-3
	0.00	0.34	0.38	0.25	0.24	0.62	0.59
	-	0-2	0-3	0-3	0-4	0-4	0-3
carry	0.03	0.16	0.31	0.43	0.24	0.54	0.41
	0-1	0-1	0-3	0-6	0-2	0-3	0-3
	0.03	0.16	0.31	0.38	0.24	0.39	0.35
	0-1	0-1	0-3	0-5	0-2	0-2	0-3
root	0.68	6.53	12.56	19.43	9.35	14.23	20.12
	0-7	0-39	0-41	0-96	0-56	0-55	0-58
	0.58	5.25	10.25	13.25	7.44	13.23	16.00
	0-5	0-23	0-30	0-47	0-47	0-39	0-48

Appendix B.2 (continued)

Behaviour pattern	1-8	9-17	18-27	28-41	42-55	56-69	70-91
shovel	0.84	1.38	1.25	1.80	1.30	0.31	2.77
	0-6	0-9	0-8	0-14	0-6	0-2	0-15
	0.97	1.22	1.13	1.58	1.24	0.31	2.65
	0-9	0-7	0-6	0-8	0-6	0-2	0-13
drink water	0.03	0.16	0.13	0.90	0.78	4.23	4.00
	0-1	0-4	0-4	0-6	0-6	0-18	0-16
	0.03	0.16	0.09	0.83	0.57	2.69	2.79
	0-1	0-4	0-3	0-6	0-5	0-7	0-9
eat food	0.00	0.41	1.16	0.90	1.54	2.23	1.18
	-	0-6	0-12	0-11	0-35	0-12	0-25
	0.00	0.41	0.94	0.70	1.37	1.85	0.85
	-	0-6	0-8	0-8	0-30	0-12	0-16
chew	1.08	2.97	4.16	4.88	5.74	5.31	5.71
	0-7	0-13	0-15	0-14	0-20	0-14	0-19
	1.00	2.59	3.91	4.20	5.76	5.08	5.09
	0-6	0-11	0-16	0-13	0-25	0-12	0-14
paw	0.55	1.09	1.34	0.58	0.70	0.08	0.12
	0-8	0-9	0-10	0-9	0-9	0-1	0-2
	0.45	0.91	1.06	0.45	0.50	0.08	0.12
	0-5	0-7	0-7	0-8	0-6	0-1	0-2
push past	5.58	4.84	2.38	1.75	2.37	1.00	1.09
	1-17	0-21	0-10	0-6	0-11	0-8	0-11
	5.18	4.84	2.34	1.75	2.28	1.00	1.00
	1-16	0-21	0-10	0-6	0-10	0-8	0-7
climb on pig	0.26	0.28	0.25	0.15	0.22	0.08	0.00
	0-2	0-4	0-3	0-2	0-2	0-1	-
	0.26	0.22	0.22	0.15	0.22	0.08	0.00
	0-2	0-3	0-3	0-2	0-2	0-1	-
lie contact on belly	5.18	4.84	2.03	2.30	1.70	2.39	1.12
	0-18	0-19	0-11	0-10	0-9	0-14	0-8
	17.42	7.78	12.09	10.00	5.41	2.23	2.68
	0-59	0-53	0-58	0-59	0-59	0-11	0-47
lie contact on side	0.24	0.06	0.09	0.20	0.04	0.00	0.35
	0-3	0-1	0-2	0-5	0-1	-	0-12
	1.21	0.06	0.13	0.18	0.02	0.00	0.35
	0-39	0-1	0-3	0-5	0-1	-	0-12
sit contact	4.11	3.47	1.25	1.13	1.54	0.62	0.38
	0-18	0-20	0-8	0-9	0-14	0-5	0-8
	5.21	3.22	1.13	1.03	2.09	0.62	0.29
	0-41	0-15	0-7	0-8	0-32	0-4	0-6
kneel contact	0.32	0.63	0.13	0.53	0.26	0.23	0.27
	0-4	0-5	0-1	0-5	0-2	0-1	0-2
	0.32	0.53	0.13	0.48	0.26	0.23	0.24
	0-4	0-4	0-1	0-4	0-2	0-1	0-2
stand contact	8.26	9.84	3.59	2.85	5.30	2.62	2.06
	0-21	0-33	0-16	0-9	0-26	0-17	0-13
	9.53	9.78	3.47	3.53	6.50	3.15	2.21
	0-42	0-55	0-24	0-45	0-52	0-26	0-22
knock	0.37	0.66	0.66	0.88	0.78	0.69	0.94
	0-2	0-3	0-4	0-5	0-6	0-3	0-4
	0.37	0.66	0.59	0.80	0.70	0.69	0.94
	0-2	0-3	0-3	0-4	0-4	0-3	0-4

Appendix B.2 (continued)

Behaviour pattern	1-8	9-17	18-27	28-41	42-55	56-69	70-91
bite	0.71	0.94	0.22	0.45	0.37	0.54	0.56
	0-7	0-5	0-1	0-2	0-4	0-2	0-3
	0.63	0.91	0.22	0.43	0.37	0.54	0.56
	0-4	0-5	0-1	0-2	0-4	0-2	0-3
push heads, parallel	0.32	0.69	1.38	1.13	0.44	0.62	0.77
	0-3	0-5	0-6	0-11	0-3	0-2	0-4
	0.45	0.66	1.16	1.03	0.44	0.62	0.77
	0-4	0-4	0-5	0-8	0-3	0-2	0-4
push heads, opposing	0.11	0.50	0.69	1.73	0.41	0.46	0.56
	0-3	0-5	0-4	0-15	0-6	0-3	0-4
	0.11	0.50	0.63	1.45	0.37	0.46	0.50
	0-3	0-5	0-3	0-11	0-4	0-3	0-3
circle	0.26	0.53	0.56	0.83	0.24	0.31	0.24
	0-8	0-4	0-4	0-6	0-3	0-3	0-2
	0.68	0.53	0.56	0.75	0.24	0.23	0.24
	0-19	0-4	0-4	0-4	0-3	0-2	0-2
shove head	0.61	0.78	1.38	1.58	0.94	0.46	1.24
	0-4	0-6	0-9	0-7	0-8	0-3	0-8
	0.61	0.78	1.22	1.58	0.87	0.46	1.18
	0-4	0-6	0-7	0-7	0-7	0-3	0-7
shove body	0.26	0.50	0.81	0.95	0.39	1.00	1.50
	0-2	0-4	0-6	0-8	0-4	0-7	0-8
	0.26	0.47	0.78	0.80	0.35	0.92	1.21
	0-2	0-3	0-5	0-6	0-3	0-6	0-6
lever body	0.08	0.22	0.18	0.16	0.06	0.16	0.12
	0-1	0-2	0-2	0-1	0-1	0-1	0-1
	0.08	0.22	0.18	0.16	0.06	0.16	0.12
	0-1	0-2	0-2	0-1	0-1	0-1	0-1
turn away	1.21	3.53	3.03	2.18	2.63	2.54	3.88
	0-10	0-18	0-13	0-8	0-10	0-7	0-12
	1.13	3.38	2.81	2.00	2.52	2.31	3.68
	0-8	0-17	0-12	0-7	0-8	0-6	0-11
chase	0.08	0.22	0.09	0.13	0.04	0.00	0.06
	0-1	0-3	0-2	0-2	0-1	-	0-1
	0.08	0.22	0.09	0.13	0.04	0.00	0.06
	0-1	0-3	0-2	0-2	0-1	-	0-1
orient towards	0.42	2.00	1.38	2.90	2.54	3.77	5.41
	0-4	0-8	0-4	0-12	0-11	0-9	0-14
	0.42	2.00	1.31	2.73	2.54	3.69	5.35
	0-4	0-8	0-4	0-10	0-10	0-9	0-14
sniff noses	0.58	1.16	2.09	1.38	1.15	2.23	1.74
	0-3	0-4	0-14	0-6	0-5	0-5	0-6
	0.58	1.09	1.94	1.33	1.11	2.08	1.62
	0-3	0-4	0-10	0-6	0-4	0-4	0-5
sniff head	1.32	2.06	1.19	1.90	2.44	2.62	2.18
	0-8	0-6	0-7	0-11	0-11	0-6	0-10
	1.26	1.78	1.19	1.70	2.28	2.46	1.97
	0-8	0-6	0-7	0-8	0-10	0-6	0-8
sniff body	1.61	2.28	1.63	1.43	1.13	1.69	1.06
	0-11	0-12	0-8	0-9	0-5	0-5	0-7
	1.63	2.03	1.44	1.35	1.09	1.54	1.06
	0-10	0-7	0-7	0-9	0-5	0-3	0-6

Appendix B.2 (continued)

Behaviour patterns	1-8	9-17	18-27	28-41	42-55	56-69	70-91
chew head	0.42	0.41	0.09	0.05	0.11	0.54	0.09
	0-4	0-3	0-1	0-1	0-2	0-3	0-1
	0.40	0.41	0.09	0.05	0.11	0.54	0.09
	0-4	0-3	0-1	0-1	0-2	0-2	0-1
chew body	0.16	0.41	0.28	0.18	0.04	0.08	0.00
	0-2	0-3	0-5	0-1	0-1	0-1	-
	0.16	0.38	0.25	0.50	0.04	0.08	0.00
	0-2	0-3	0-4	0-14	0-1	0-1	-
anogenital sniff	0.00	0.06	0.06	0.08	0.07	0.15	0.09
	-	0-1	0-1	0-1	0-1	0-1	0-1
	0.00	0.06	0.06	0.08	0.07	0.15	0.09
	-	0-1	0-1	0-1	0-1	0-1	0-1
attempted mount	0.00	0.00	0.03	0.05	0.00	0.00	0.06
	-	-	0-1	0-1	-	-	0-1
	0.00	0.00	0.03	0.05	0.00	0.00	0.06
	-	-	0-1	0-1	-	-	0-1
mount side	0.03	0.03	0.09	0.10	0.02	0.08	0.03
	0-1	0-1	0-2	0-2	0-1	0-1	0-1
	0.03	0.03	0.09	0.10	0.02	0.08	0.03
	0-1	0-1	0-2	0-2	0-1	0-1	0-1
mount side	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	-	-	-	-	-	-	-
	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	-	-	-	-	-	-	-
sniff udder	2.32	1.00	0.56	0.38	0.91	0.08	0.06
	0-8	0-5	0-3	0-3	0-10	0-1	0-1
	4.76	0.91	0.50	0.35	0.89	0.08	0.06
	0-51	0-4	0-3	0-2	0-10	0-1	0-1
suck teat	7.90	4.59	2.69	2.83	3.80	1.23	0.65
	0-52	0-25	0-20	0-15	0-21	0-6	0-8
	7.47	4.59	2.31	2.65	3.30	1.00	0.59
	0-51	0-33	0-12	0-29	0-21	0-5	0-5
drink milk	0.45	0.47	0.38	0.45	0.52	0.15	0.18
	0-2	0-1	0-2	0-3	0-6	0-1	0-3
	0.42	0.47	0.38	0.40	0.33	0.15	0.12
	0-1	0-1	0-1	0-1	0-1	0-1	0-1
switch teats	2.45	1.94	0.34	0.80	1.09	0.00	0.06
	0-23	0-22	0-5	0-16	0-18	-	0-2
	1.45	0.59	0.16	0.28	0.37	0.00	0.03
	0-13	0-6	0-2	0-4	0-4	-	0-1
push for unexposed teat	0.92	0.31	0.09	0.15	0.28	0.00	0.03
	0-7	0-2	0-2	0-4	0-3	-	0-1
	0.90	0.31	0.06	0.15	0.28	0.00	0.03
	0-7	0-2	0-2	0-4	0-3	-	0-1
orient towards udder	0.42	0.84	0.72	0.43	0.59	0.92	0.09
	0-9	0-4	0-4	0-5	0-3	0-6	0-1
	0.42	0.72	0.72	0.38	0.59	0.62	0.09
	0-9	0-4	0-4	0-2	0-4	0-4	0-1
fight for teats	0.92	0.06	0.06	0.03	0.08	0.00	0.00
	0-5	0-1	0-2	0-1	0-2	-	-
	0.85	0.06	0.06	0.03	0.06	0.00	0.00
	0-4	0-1	0-2	0-1	0-1	-	-

Appendix B.2 (continued)

Behaviour patterns	1-8	9-17	18-27	28-41	42-55	56-69	70-91
receive threat from sow	0.00 - 0.00 -	0.03 0-1 0.03 0-1	0.06 0-1 0.06 0-1	0.08 0-1 0.08 0-1	0.20 0-4 0.15 0-2	0.23 0-2 0.23 0-2	0.24 0-2 0.24 0-2
sniff udder of another sow	0.00 - 0.00 -	0.25 0-3 0.03 0-1	0.16 0-2 0.03 0-1	0.16 0-2 0.08 0-1	0.50 0-5 0.33 0-3	0.31 0-2 0.31 0-2	0.03 0-1 0.03 0-1
No. of 30 minute focal samples	38	32	32	40	46	26	34

Appendix C.1 Significant transitions performed during non-play in the Pig Park (1-8 days)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
stand apart	step	**
	walk	**
	slow grunting	**
	rapid grunting	**
	headshake	*
step	stand apart	*
	walk	**
walk	stand apart	**
	slow grunting	**
	rapid grunting	**
	sniff ground	**
	sniff object	**
	sniff head	*
	sniff body	*
slow grunting	stand apart	**
	step	*
	walk	*
	sniff ground	*
rapid grunting	stand apart	*
	step	*
	walk	*
squeak	lie contact on belly	*
headshake	sniff ground	*
sniff ground	walk	**
sniff object	step	*
	walk	*
root	walk	*
push past	lie contact on belly	**
	stand contact	**
	sniff udder	**
	suck teat	*
receive push past	lie contact on belly	**
	stand contact	**
	suck teat	**
lie contact on belly	squeak	*
	receive push past	**
	sit contact	**
	stand contact	**
	suck teat	*
sit contact	receive push past	**
	lie contact on belly	**
	stand contact	**
	suck teat	**
stand contact	headshake	*
	push past	**
	sit contact	*
	sniff udder	*
sniff head	step	**
sniff body	walk	*
sniff udder	push past	**
	suck teat	**
suck teat	receive push past	**
	lie contact on belly	**
	sit contact	**
	sniff udder	**
	switch teats	**
	push for unexposed teat	**
switch teats	suck teat	**

Appendix C.2 Significant transitions performed during non-play in the Pig Park (9-17 days)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
stand apart	step	*
	walk	**
	sniff ground	*
step	stand apart	*
	walk	**
	root	*
	chew	*
walk	stand apart	*
	trot	**
	slow grunting	**
	rapid grunting	**
	sniff, bite observer	*
	sniff ground	**
	walk sniffing ground	*
	sniff object	*
	orient towards	*
	sniff body	*
	sniff udder	**
trot	walk	**
slow grunting	step	*
	sniff ground	*
	walk sniffing ground	*
	root	**
rapid grunting	stand apart	*
	walk	*
sniff ground	kneel apart	*
	walk	*
	slow grunting	*
	sniff object	*
	shovel	*
	chew	*
	paw	*
	receive push past	*
	receive orientation towards	**
root	step	**
	slow grunting	*
paw	sniff ground	**
push past	lie contact on belly	**
	sit contact	**
	stand contact	**
receive push past	lie contact on belly	**
	stand contact	*
lie contact on belly	receive push past	**
	sit contact	**
	stand contact	**
	suck teat	*
sit contact	lie contact on belly	**
	stand contact	**
stand contact	rapid grunting	*
	push past	**
	sit contact	*
receive orientation towards	step	*
	stand contact	*
sniff noses	walk	*
sniff head	step	*
sniff body	step	*
suck teat	lie contact on belly	*

Appendix C.3 Significant transitions performed during non-play in the Pig Park (18-91 days) (significance of transitions common to play shown in brackets)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
kneel apart	stand apart	**
stand apart	walk	**
	slow grunting	**
	rapid grunting	*(*)
	cough, sneeze	**
	headshake	**
	urinate	**
	defecate	**
	orient towards observer	**
	receive sniff at head	*
step	orient towards observer	**
	sniff, bite observer	**(**)
	sniff ground	**
	root	**(**)
	drink water	**
walk	stand apart	**
	trot	**(**)
	crawl on belly	*
	slow grunting	**(**)
	rapid grunting	**(**)
	wag tail	**(**)
	defecate	*
	sniff, bite observer	*
	sniff ground	**(**)
	sniff object	**
	root	*
	drink water	**
	push heads, parallel	*
	orient towards	**(**)
	sniff noses	**
	suck teat	**
	orient towards udder	*
trot	walk	**
	slow grunting	**
	rapid grunting	**(*)
	wag tail	**
slow grunting	stand apart	**
	walk	**
	trot	**(*)
	sniff ground	**
	walk sniffing ground	*
	sniff, bite observer	*
rapid grunting	stand apart	**(*)
	walk	**
	trot	**(*)
	sniff noses	**
whine	stand contact	**
	turn away	**
wag tail	sniff ground	**(*)
	root	**(*)
	shove head	*
	orient towards	**(**)
cough, sneeze	stand apart	*
	walk	*
	sniff ground	*
headshake	wag tail	**(*)
rub body	stand apart	*
	step	*
	walk	*
urinate	sniff ground	**

Appendix C.3 (continued)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
defecate	walk	**
	sniff ground	*
orient towards observer	step	**
sniff, bite observer	step	**(*)
	walk	*
sniff ground	step	**(**)
	walk	**(**)
	walk sniffing ground	**(**)
	tug, brace object	*
	shovel	**
	chew	**
	paw	**
	receive orientation towards	*
walk sniffing ground	slow grunting	*
	defecate	*
	sniff ground	**(*)
	root	**(**)
	drink water	*
sniff object	step	*
	bite object	**
bite object	sniff object	**
	shovel	**
	chew	*
	receive push past	*
	receive orientation towards	**
	receive sniff at head	*
tug, brace object	sniff ground	**
carry	walk	**(**)
root	kneel apart	**
	step	**(**)
	walk	**(*)
	cough, sneeze	*
	walk sniffing ground	**(**)
	bite object	**
	shovel	**
	chew	**
	receive push past	*
	receive shove at head	**
	receive orientation towards	**(**)
	receive sniff at head	*
shovel	bite object	*
	root	*
	receive orientation towards	*
drink water	stand apart	**
	step	**
eat food	step	**
	chew	**
	turn away	*
chew	step	**(**)
	scratch	*
	sniff ground	**(*)
	eat food	**
	receive sniff at head	**
paw	sniff ground	**
push past	lie contact on belly	**
	stand contact	**
	suck teat	**
receive push past	stand contact	**
	turn away	**
lie contact on belly	stand contact	**
	receive orientation towards	**
	sniff head	*
	suck teat	**

Appendix C.3 (continued)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
sit contact	stand contact	**
stand contact	step	*
	headshake	*
	push past	**
	receive push past	**
	lie contact on belly	**
	sit contact	**
	sniff head	*
	receive sniff at head	*
	suck teat	*
turn away	walk	**(**)
	whine	**
	root	*(*)
	chew	*
	lie contact on belly	*
	sit contact	**
receive turn away	sniff ground	*
	root	**(*)
	sniff head	*
receive shove at body	walk	*
orient towards	root	*
	eat food	*
	receive turn away	**
	receive orientation towards	**
	sniff noses	*
receive orientation towards	root	**(*)
	lie contact on belly	*
	turn away	**
sniff noses	stand contact	*
	turn away	**
sniff head	push past	**
	stand contact	*
	receive turn away	**
receive sniff at head	turn away	**
sniff body	stand contact	*
suck teat	stand apart	**
	receive push past	*
	lie contact on belly	**
	stand contact	**
orient towards udder	walk	*

Appendix C.4 Transitions significant only during play in the Pig Park (18-91 days)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
stand apart	pivot	**
step	sniff object	**
	chew	**
	shove head	*
	shove body	*
trot	gallop	*
	scamper	**
gallop	stand apart	**
	pivot	**
	rapid grunting	*
scamper	stand apart	**
	trot	**
	gallop	**
	alert stance	**
	pivot	*
	bump	**
	rapid grunting	**
	bark	**
hop	stand apart	**
	walk	*
pivot	stand apart	**
	toss head	**
	alert stance	*
	wag tail	**
toss head	pivot	**
slow grunting	scamper	*
rapid grunting	gallop	*
	scamper	**
bark	scamper	**
wag tail	toss head	**
	shove body	**
headshake	root	*
scratch	sniff ground	*
sniff ground	slow grunting	*
	shake object	**
bite object	wag tail	*
eat food	walk	*
turn away	scamper	*
sniff head	step	*
receive sniff at head	walk	*
sniff body	step	*

Appendix D Behavioural frequencies of piglets in the incubators and flat-deck cages

(A) mean frequency (times/30 min), (B) range (times/30 min), (C) mean no. 30 sec intervals/30 min and (D) range (intervals/30 min) during each age period (days)

Behaviour pattern		In incubators 1-8	In incubators 9-17	In flat-deck cages 18-27 Incub. reared (I.R.)	In flat-deck cages 18-27 Sow reared (S.R.)	In flat-deck cages 28-41 I.R.	In flat-deck cages 28-41 S.R.
lie apart on belly	A	3.28	13.35	1.19	3.42	2.33	7.21
	B	0-27	0-55	0-11	0-25	0-18	0-49
	C	35.98	22.71	0.76	2.75	1.87	7.85
	D	0-60	0-60	0-6	0-19	0-15	0-54
lie apart on belly		0.51	0.66	0.05	0.17	0.03	0.52
		0-6	0-7	0-1	0-2	0-1	0-12
		4.28	2.76	0.05	0.17	0.03	0.46
		0-59	0-54	0-1	0-2	0-1	0-10
sit apart		1.93	8.64	1.52	1.21	1.13	1.42
		0-12	0-38	0-9	0-5	0-7	0-12
		2.84	7.11	1.43	0.13	1.03	1.21
		0-12	0-29	0-7	0-5	0-6	0-7
kneel apart		0.47	2.16	1.33	1.54	1.83	4.61
		0-3	0-13	0-6	0-6	0-16	0-37
		0.47	2.13	1.14	1.33	1.63	3.82
		0-3	0-12	0-5	0-5	0-13	0-27
stand apart		11.93	18.02	21.00	31.71	21.43	26.79
		0-95	0-76	0-60	0-99	3-68	0-77
		12.21	12.91	16.24	20.58	14.73	17.70
		0-59	0-43	0-42	0-50	3-21	0-43
alert stance		0.14	0.88	0.05	0.77	0.30	1.18
		0-2	0-5	0-1	0-6	0-1	0-16
		0.10	0.84	0.05	0.59	0.30	0.85
		0-1	0-5	0-1	0-5	0-1	0-8
step, walk		9.14	14.38	53.95	48.17	55.30	50.88
		0-121	0-75	0-137	0-83	5-127	0-114
		6.23	9.62	28.00	27.67	28.93	28.52
		0-48	0-33	0-53	0-48	3-52	0-50
trot, gallop		0.02	0.09	1.10	0.92	2.57	1.24
		0-1	0-3	0-10	0-6	0-17	0-15
		0.02	0.06	0.71	0.92	1.30	0.85
		0-1	0-2	0-5	0-6	0-8	0-7
slip, fall		0.77	2.13	0.48	0.13	0.23	0.12
		0-8	0-9	0-2	0-2	0-2	0-2
		0.74	2.02	0.48	0.13	0.23	0.12
		0-8	0-8	0-2	0-2	0-2	0-2
crawl on belly		0.49	1.06	0.14	0.58	0.13	0.15
		0-5	0-7	0-1	0-3	0-2	0-2
		0.47	0.98	0.14	0.54	0.13	0.15
		0-4	0-6	0-1	0-3	0-2	0-2
climb		0.02	0.13	2.19	1.83	4.33	1.39
		0-1	0-7	0-16	0-18	0-27	0-8
		0.02	0.07	1.33	1.38	3.00	1.12
		0-1	0-4	0-12	0-12	0-16	0-7
scamper		0.00	0.20	1.48	0.54	2.27	1.49
		-	0-7	0-22	0-7	0-21	0-11
		0.00	0.16	0.76	0.38	1.27	0.97
		-	0-5	0-10	0-3	0-12	0-7

Appendix D (continued)

Behaviour pattern	1-8	9-17	18-27		28-41	
			I.R.	S.R.	I.R.	S.R.
hop	0.09	0.46	0.67	1.25	1.30	0.94
	0-2	0-7	0-7	0-14	0-17	0-6
	0.09	0.40	0.57	0.96	1.00	0.79
	0-2	0-6	0-5	0-7	0-11	0-6
pivot	0.05	1.11	1.48	1.58	1.73	1.70
	0-1	0-19	0-16	0-13	0-18	0-13
	0.05	0.75	1.10	0.96	1.27	1.24
	0-1	0-7	0-9	0-7	0-11	0-9
toss head	0.00	1.60	1.76	1.17	1.90	1.70
	-	0-17	0-16	0-6	0-13	0-11
	0.00	1.09	1.14	1.00	1.53	1.39
	-	0-10	0-7	0-5	0-9	0-6
flop on side, belly	0.00	0.40	0.19	0.13	0.03	0.09
	-	0-4	0-2	0-1	0-1	0-1
	0.00	0.38	0.19	0.13	0.03	0.09
	-	0-4	0-2	0-1	0-1	0-1
bump	not possible in incubators		0.43	0.25	0.97	0.67
			0-5	0-2	0-9	0-6
			0.22	0.25	0.67	0.61
			0-5	0-2	0-8	0-6
slow grunting	2.72	11.60	9.62	25.29	17.20	21.06
	0-18	0-114	0-67	0-115	0-125	0-117
	2.07	7.86	6.38	13.96	10.37	12.21
	0-15	0-56	0-37	0-46	0-52	0-47
rapid grunting	0.49	0.75	0.76	2.83	0.80	0.67
	0-17	0-14	0-7	0-26	0-8	0-10
	0.98	0.62	0.76	2.17	0.70	0.58
	0-10	0-11	0-7	0-17	0-8	0-8
quack	0.07	0.00	0.14	0.08	0.07	0.00
	0-2	-	0-2	0-2	0-1	-
	0.07	0.00	0.14	0.08	0.02	0.00
	0-2	-	0-2	0-2	0-1	-
whine	1.56	6.46	3.48	6.67	5.50	2.36
	0-61	0-84	0-15	0-45	0-34	0-14
	0.84	3.64	2.52	4.38	3.57	2.12
	0-31	0-43	0-9	0-24	0-16	0-10
squeak	2.79	1.44	0.81	5.75	0.20	3.52
	0-46	0-18	0-4	0-45	0-2	0-39
	2.40	1.16	0.67	3.83	0.20	2.24
	0-42	0-14	0-3	0-27	0-2	0-22
squeal	not possible in incubators		0.19	0.79	0.27	0.49
			0-2	0-5	0-1	0-9
			0.19	o.58	0.27	0.36
			0-2	0-3	0-1	0-5
scream	0.02	0.53	1.19	1.58	1.43	0.03
	0-1	0-15	0-16	0-22	0-22	0-1
	0.02	0.51	0.81	0.79	0.63	0.03
	0-1	0-14	0-9	0-10	0-7	0-1
bark	0.00	0.02	0.00	0.04	0.13	0.12
	-	0-1	-	0-1	0-3	0-2
	0.00	0.02	0.00	0.04	0.13	0.12
	-	0-1	-	0-1	0-3	0-2

Appendix D (continued)

Behaviour pattern	1-8	9-17	18-27		28-41	
			I.R.	S.R.	I.R.	S.R.
threatening grunt	not possible in incubators		0.10 0-1 0.10 0-1	0.17 0-2 0.08 0-1	0.10 0-1 0.10 0-1	0.12 0-2 0.12 0-2
wag tail	0.09 0-1 0.09 0-1	0.40 0-4 0.35 0-3	18.43 0-61 13.43 0-42	16.46 0-51 12.33 0-35	30.30 2-82 21.30 2-49	23.64 0-77 18.00 0-45
yawn	0.26 0-2 0.26 0-2	0.86 0-4 0.82 0-4	0.81 0-4 0.76 0-3	0.88 0-5 0.83 0-4	0.67 0-4 0.67 0-4	0.64 0-5 0.64 0-5
cough, sneeze	0.37 0-8 0.33 0-7	0.76 0-9 0.75 0-9	0.19 0-1 0.19 0-1	0.67 0-6 0.54 0-3	0.63 0-4 0.63 0-4	1.49 0-39 1.00 0-24
stretch	0.09 0-2 0.09 0-2	0.36 0-3 0.35 0-3	0.57 0-2 0.57 0-2	1.17 0-5 1.17 0-5	1.03 0-4 1.03 0-4	2.36 0-14 2.30 0-13
headshake	1.70 0-11 1.51 0-11	5.87 0-27 5.07 0-19	3.95 0-9 3.71 0-9	4.04 0-15 3.58 0-11	5.83 0-18 5.37 0-15	3.18 0-10 3.03 0-10
scratch	0.05 0-2 0.05 0-2	0.81 0-10 0.73 0-10	4.90 0-17 4.05 0-13	3.37 0-8 2.87 0-5	3.47 0-20 2.77 0-14	2.19 0-6 2.07 0-5
rub head	0.05 0-2 0.05 0-2	0.55 0-6 0.47 0-6	0.05 0-1 0.05 0-1	0.08 0-1 0.08 0-1	0.10 0-2 0.10 0-2	0.03 0-1 0.03 0-1
rub body	0.00 - 0.00 -	0.22 0-3 0.22 0-3	1.34 0-7 1.24 0-7	0.79 0-3 0.75 0-3	1.06 0-8 1.03 0-8	0.55 0-4 0.49 0-3
urinate	0.14 0-2 0.14 0-2	0.07 0-2 0.07 0-2	0.91 0-4 0.62 0-2	0.75 0-4 0.58 0-3	1.40 0-8 1.20 0-7	0.88 0-4 0.76 0-3
defecate	0.07 0-2 0.07 0-2	0.00 - 0.00 -	0.43 0-3 0.38 0-3	0.38 0-3 0.33 0-3	0.37 0-2 0.37 0-2	0.33 0-2 0.33 0-2
orient towards observer	0.58 0-15 0.51 0-12	1.80 0-12 1.80 0-12	3.71 0-18 3.14 0-13	6.29 0-20 5.08 0-13	4.37 0-22 3.53 0-15	2.67 0-11 2.49 0-9
sniff floor	4.42 0-34 3.16 0-24	14.56 0-54 10.13 0-47	17.10 0-70 12.19 0-38	21.58 0-58 14.38 0-33	22.80 0-75 15.53 0-43	31.00 0-74 20.88 0-40

Appendix D (continued)

Behaviour pattern	1-8	9-17	18-27 I.R.	S.R.	28-41 I.R.	S.R.
walk	0.07	0.07	2.43	2.58	2.20	4.03
sniffing floor	0-3	0-2	0-21	0-9	0-8	0-18
	0.07	0.07	2.00	2.17	2.00	3.64
	0-3	0-2	0-16	0-7	0-8	0-17
sniff faeces	not distinguishable from sniff floor in incubators		0.19	0.17	0.93	1.49
			0-2	0-3	0-23	0-11
			0.19	0.17	0.57	1.12
			0-2	0-3	0-12	0-8
sniff urine			0.05	0.54	0.20	3.91
			0-1	0-9	0-2	0-87
			0.05	0.38	0.17	1.91
			0-1	0-7	0-1	0-33
sniff window	2.51	7.58	not possible in flat-deck cages			
	0-17	0-42				
	2.00	6.73				
	0-13	0-53				
sniff object	2.56	6.91	21.95	26.00	37.57	32.39
(walls, ceiling,	0-33	0-24	0-61	0-70	5-84	0-79
trough)	1.93	5.33	14.29	16.33	22.10	19.76
	0-25	0-19	0-30	0-41	5-42	0-42
sniff nipple	4.23	9.07	3.38	3.58	5.20	2.85
drinker	0-27	0-38	0-8	0-10	0-38	0-13
	3.14	7.27	2.81	3.21	4.13	2.42
	0-20	0-25	0-5	0-10	0-29	0-12
bite, lick object	0.35	5.77	5.24	7.33	6.33	16.82
(floor, walls,	0-4	0-25	0-28	0-37	0-19	0-79
trough)	0.35	4.78	5.24	5.46	5.23	10.97
	0-4	0-20	0-36	0-23	0-15	0-39
push at window	4.42	20.18	not possible in flat-deck cages			
	0-94	0-134				
	2.61	11.82				
	0-51	0-55				
root, lever	3.82	12.37	14.48	6.75	23.10	24.15
(floor, walls,	0-39	0-79	0-54	0-25	2-66	0-85
trough)	4.23	8.93	9.24	5.29	15.53	14.91
	0-54	0-36	0-33	0-16	2-31	0-47
shovel (food)	0.00	0.00	2.24	1.29	0.93	0.33
	-	-	0-14	0-22	0-9	0-7
	0.00	0.00	1.49	0.71	0.80	0.21
	-	-	0-7	0-10	0-8	0-3
suck, manipulate	3.33	20.13	1.48	1.00	1.07	1.00
nipple drinker	0-37	0-88	0-7	0-6	0-7	0-6
	2.56	13.53	1.05	1.00	0.87	0.85
	0-23	0-55	0-5	0-6	0-7	0-6
drink from	0.33	1.27	5.62	2.96	8.30	3.52
nipple drinker	0-4	0-20	0-16	0-16	0-40	0-16
	0.30	0.84	3.62	2.21	6.93	3.30
	0-3	0-10	0-11	0-13	0-29	0-15
massage nipple	1.14	18.06	2.05	0.00	6.10	0.00
drinker, area	0-25	0-145	0-13	-	0-50	-
around it	0.65	8.78	1.19	0.00	4.50	0.00
	0-21	0-50	0-4	-	0-38	-

Appendix D (continued)

Behaviour pattern	1-8	9-17	18-27 I.R.	18-27 S.R.	28-41 I.R.	28-41 S.R.
eat, drink from trough	1.65 0-19 1.47 0-16	5.87 0-63 5.02 0-50	19.81 0-81 12.19 0-42	19.79 0-45 12.17 0-31	31.90 0-116 19.93 0-46	22.03 0-103 11.88 0-49
chew (food)	2.02 0-25 1.58 0-15	8.60 0-65 6.56 0-34	21.00 0-105 13.52 0-49	26.08 0-108 16.67 0-56	26.47 2-92 17.83 2-49	27.00 0-114 17.00 0-43
paw	0.14 0-3 0.12 0-2	2.47 0-29 1.69 0-15	2.14 0-8 1.29 0-4	2.13 0-20 1.21 0-9	3.13 0-20 2.23 0-14	1.67 0-13 1.27 0-8
nose, chew own body	0.00 - 0.00 -	3.16 0-30 2.27 0-20	0.24 0-2 0.24 0-2	0.25 0-2 0.17 0-1	0.70 0-6 0.60 0-5	0.73 0-8 0.61 0-8
push past partner			4.05 0-15 3.90 0-14	3.21 0-9 2.88 0-9	5.23 0-17 4.80 0-15	2.70 0-13 2.49 0-11
climb on partner			0.52 0-8 0.48 0-7	0.38 0-3 0.38 0-3	0.10 0-2 0.10 0-2	0.36 0-2 0.36 0-2
lie contact on belly			1.10 0-10 2.81 0-39	5.79 0-25 8.71 0-59	1.57 0-16 1.83 0-16	5.61 0-27 5.30 0-37
lie contact on side			0.10 0-1 2.67 0-55	0.79 0-12 0.71 0-10	0.10 0-3 0.07 0-2	0.70 0-6 0.64 0-6
sit contact	not possible in incubators		3.10 0-17 2.33 0-12	1.79 0-9 1.63 0-8	1.47 0-12 1.17 0-6	1.46 0-12 1.42 0-12
kneel contact			0.71 0-4 0.71 0-3	0.79 0-5 0.75 0-4	0.80 0-7 0.70 0-5	0.52 0-5 0.49 0-5
stand contact			8.19 0-29 7.14 0-35	8.58 0-41 6.63 0-33	9.37 0-30 6.83 0-21	4.18 0-17 3.21 0-11
knock			0.91 0-4 0.91 0-4	2.42 0-12 1.92 0-10	2.27 0-15 1.90 0-11	1.58 0-6 1.39 0-4
bite			1.19 0-5 1.05 0-4	0.58 0-9 0.38 0-4	0.33 0-3 0.33 0-3	0.42 0-3 0.39 0-2

Appendix D (continued)

Behaviour pattern	1-8	9-17	18-27 I.R.	S.R.	28-41 I.R.	S.R.
push heads, parallel			3.62	1.13	1.70	0.94
			0-10	0-7	0-6	0-5
			3.24	1.00	1.57	0.91
			0-8	0-6	0-5	0-4
push heads, opposing			8.43	2.54	2.93	2.49
			0-21	0-16	0-18	0-13
			6.43	2.17	2.43	1.73
			0-13	0-13	0-13	0-9
circle			8.10	1.50	0.57	0.52
			0-62	0-10	0-3	0-7
			5.86	1.25	0.63	0.46
			0-39	0-8	0-3	0-6
shove head			2.62	1.46	2.00	2.03
			0-9	0-6	0-6	0-6
			2.38	1.38	1.77	1.70
			0-7	0-6	0-6	0-5
shove body			2.14	1.08	1.07	0.82
			0-7	0-4	0-6	0-5
			2.00	1.08	1.03	0.76
			0-5	0-4	0-6	0-5
lever body			11.24	2.33	0.83	0.91
			0-72	0-16	0-8	0-6
			7.38	2.17	0.70	0.88
			0-40	0-10	0-5	0-6
turn away	not possible in incubators		2.52	1.63	1.60	0.82
			0-12	0-14	0-13	0-13
			2.14	1.29	1.30	0.61
			0-11	0-8	0-7	0-6
chase			0.38	0.08	0.00	0.00
			0-8	0-2	-	-
			0.38	0.08	0.00	0.00
			0-8	0-2	-	-
orient towards partner			1.76	1.29	0.73	0.70
			0-6	0-10	0-4	0-5
			1.71	1.17	0.73	0.67
			0-6	0-8	0-4	0-4
sniff noses			1.67	0.54	0.83	0.49
			0-6	0-3	0-3	0-4
			1.57	0.54	0.80	0.49
			0-6	0-3	0-3	0-4
sniff head			7.81	5.04	4.30	4.49
			0-26	0-20	0-15	0-15
			6.67	4.50	3.87	4.09
			0-21	0-15	0-13	0-13
sniff body			11.67	8.00	7.03	9.73
			0-36	0-30	0-18	0-24
			9.29	6.29	6.00	7.70
			0-29	0-22	0-16	0-19
chew head			5.52	1.54	1.87	2.64
			0-39	0-8	0-10	0-16
			3.81	1.17	1.67	2.18
			0-23	0-7	0-13	0-15

Appendix D (continued)

Behaviour pattern	1-8	9-17	18-27 I.R.	18-27 S.R.	28-41 I.R.	28-41 S.R.
chew body			3.95 0-29 3.29 0-21	2.42 0-15 1.71 0-8	1.20 0-7 1.07 0-4	2.61 0-16 2.15 0-10
anogenital sniff			0.29 0-2 0.24 0-1	0.46 0-3 0.42 0-3	0.20 0-2 0.20 0-2	1.09 0-8 1.03 0-8
attempted mount			1.43 0-9 1.43 0-9	1.17 0-5 1.04 0-4	1.13 0-5 1.13 0-5	1.21 0-6 1.15 0-5
mount side	not possible in incubators		1.33 0-11 1.05 0-6	1.08 0-8 0.92 0-6	1.47 0-12 1.07 0-7	0.39 0-4 0.36 0-3
mount rear			0.38 0-7 0.38 0-7	0.21 0-4 0.17 0-3	0.17 0-5 0.17 0-5	0.06 0-1 0.06 0-1
massage belly of partner			0.29 0-3 0.24 0-3	0.63 0-6 0.38 0-4	0.03 0-1 0.03 0-1	0.52 0-4 0.42 0-4
massage head of partner			6.86 0-139 2.91 0-55	1.17 0-18 0.58 0-4	1.33 0-7 2.20 0-30	0.79 0-6 0.67 0-4
massage (other parts of) body of partner			13.29 0-91 8.62 0-43	2.88 0-38 1.58 0-14	4.80 0-23 3.67 0-17	5.24 0-40 4.24 0-43
No. of 30 minute focal samples	43	54	21	24	30	33

Appendix E Significant transitions performed during play and non-play in the incubators (9-17 days)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
lie apart on belly	sit apart	**
	crawl on belly	**
	yawn	**
	orient towards observer	**
	sniff floor	**
	sniff object	**
	root, lever	*
	chew food	**
	nose, chew own body	**
sit apart	lie apart on belly	**
	step, walk	*
	pivot	*
	toss head	**
	sniff object	**
	bite object	*
	suck nipple drinker	**
	drink from nipple drinker	*
	nose, chew own body	*
kneel apart	lie apart on belly	**
	sniff floor	*
stand apart	step, walk	**
	slow grunting	**
	rapid grunting	**
	squeak	*
	orient towards observer	*
	sniff window	*
	sniff object	**
step, walk	sit apart	*
	kneel apart	**
	stand apart	**
	slow grunting	**
	whine	**
	sniff floor	**
	sniff window	**
	sniff object	**
	root, lever	**
slip, fall	lie apart on belly	**
	sit apart	*
	step, walk	*
	push at window	*
crawl on belly	lie apart on belly	**
pivot	sit apart	**
	sniff floor	*
toss head	sniff object	*
	root, lever	**
slow grunting	stand apart	**
	step, walk	*
	whine	*
	orient towards observer	*
	sniff window	*
	root, lever	*
	eat from trough	**
	chew food	*
rapid grunting	stand apart	*
whine	kneel apart	*
	step, walk	**
	sniff window	**
	sniff object	*
	push at window	**
squeak	stand apart	*
	step, walk	*

Appendix E (continued)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
scream	push at window	**
yawn	lie apart on belly	**
headshake	sit apart	*
	step, walk	**
orient towards observer	sit apart	*
	sniff window	**
sniff floor	lie apart on belly	**
	kneel apart	**
	step, walk	**
	crawl on belly	*
	pivot	*
	toss head	*
	scratch	*
	sniff object	**
	bite object	**
	root, lever	**
	nose, chew own body	**
sniff window	whine	**
	orient towards observer	**
	sniff nipple drinker	**
	chew food	*
sniff object	lie apart on belly	**
	sit apart	**
	step, walk	**
	sniff floor	**
	bite object	**
	root, lever	**
sniff nipple drinker	step, walk	*
	headshake	**
	suck nipple drinker	**
	root, lever	**
	eat from trough	**
bite object	sit apart	*
	sniff object	**
	root, lever	**
push at window	slip, fall	**
	squeak	*
	scream	**
	suck nipple drinker	**
	massage nipple drinker	**
root, lever	lie apart on belly	**
	sit apart	*
	step, walk	*
	toss head	**
	whine	**
	bite object	**
	eat from trough	**
	chew food	**
	paw	**
	nose, chew own body	**
suck nipple drinker	slip, fall	*
	push at window	**
	drink from nipple drinker	**
	massage nipple drinker	**
drink from nipple drinker	lie apart on belly	*
	massage nipple drinker	**
massage nipple drinker	suck nipple drinker	**
	drink from nipple drinker	**
	eat from trough	**
eat from trough	slow grunting	**
	whine	**
	headshake	**
	root, lever	**
	chew food	**

Appendix E (continued)

Preceding behaviour	Following behaviour	Significance P < 0.05* P < 0.001**
chew food	lie apart on belly	*
	slow grunting	*
	sniff nipple drinker	*
	root, lever	*
	eat from trough	**
	nose, chew own body	*
paw	sniff object	**
	root, lever	**
nose, chew own body	lie apart on belly	**
	slow grunting	**
	sniff floor	**
	root, lever	**
	chew food	**

Appendix F Methodological and statistical techniques

SAMPLING METHODS

1 The Pig Park

Number of focal samples (n_f) and number of animals sampled (n_a) during each age period

Litter	Sow	Age period (days)													
		1-8		9-17		18-27		28-41		42-55		56-69		70-91	
		n_f	n_a	n_f	n_a	n_f	n_a	n_f	n_a	n_f	n_a	n_f	n_a	n_f	n_a
February	2	6	6	5	4	7	7	6	6	8	6	5	5	6	5
	RR	10	6	6	5	4	4	3	3	8	5	3	3	6	4
	12	6	5	7	6	9	8	5	5	14	8	5	5	9	8
June	WB	16	4	14	4	12	3	12	3	-	-	-	-	-	-
August	2	-	-	-	-	-	-	8	4	7	4	7	4	6	4
	RR	-	-	-	-	-	-	6	4	9	4	6	4	7	4
Totals		38	21	32	19	32	22	40	25	46	27	26	21	34	25

2 The incubators and flat-deck cages

Number of focal samples (n_f), number of focal animals sampled (n_{fa}), number of scan samples (n_s) and number of animals scan sampled (n_{sa}) during each age period

Piglet group	Age period (days)															
	1-8				9-17				18-27				28-41			
	n_f	n_{fa}	n_s	n_{sa}	n_f	n_{fa}	n_s	n_{sa}	n_f	n_{fa}	n_s	n_{sa}	n_f	n_{fa}	n_s	n_{sa}
Incubator-reared	43	14	10504	48	54	9	5938	34	21	9	1780	8	30	8	1236	8
Sow-reared	-	-	-	-	-	-	-	-	24	8	1764	8	33	8	1796	8

3 Behavioural categories recorded during scan samples in the incubators and flat-deck cages

Non-social behaviour	rest, stand, locomote, push window/climb, eat/chew, root, paw, drink, suck nipple drinker, massage nipple drinker, eliminate, play, comfort behaviour, grunt, high-pitched vocalization
Social behaviour (not possible in incubators)	lever/massage, lick/chew/bite, push/shove/knock, sniff, circle, mount, receive social behaviour - remain stationary, receive social behaviour - move away

Note: All categories were mutually exclusive with the exception of vocal behaviour

Appendix F (continued)

4 Social facilitation

Number of inter-individual bouts of four different types of activity

Piglet group	Age (weeks)	No. of focal samples	No. of animals sampled	No. of inter-individual bouts				Total No. of inter-individual bouts
				Rub scratch	Drink	Nose observer	Nose unusual object	
February litters	0-4	24	20	10	2	7	11	30
	4-13	40	19	42	50	25	9	126
WB's June litter	0-3	12	4	5	1	12	27	45
	3-6	9	3	5	3	8	22	38
August litters	4-13	33	24	11	25	33	14	83

Note: Focal piglets were observed in a pre-determined random order. If an animal on the list was inactive, the next active one was observed.
These focal samples, in which the activities of the animals around the focal animal were being recorded, were conducted separately from those used to collect the data discussed on pages 26-31.

Statistical tests

Sequence analysis

Data from all focal samples was lumped in first-order transition matrices according to the age and sex of the focal piglets. In the comparisons between play and non-play (pp 30-31), the sequences of behaviour occurring in play bouts and non-play bouts were lumped in separate tables. The Pig Park data was entered on 113 x 113 matrices based on the behaviour patterns listed in the ethogram (Appendix B.1). Social behaviour patterns were divided into instances of giving and receiving the behaviour. The incubator data (see Part 2), which did not include social behaviour, was lumped in 50 x 50 matrices based on the behaviour patterns listed in Appendix D. The results presented in Figure 2.5 (p 201) are based on 29 x 29 matrices, formed after lumping related behaviour patterns into single categories. All tables were incomplete in that they had structural zeros along the main diagonal. Tables of non-play sequences also had structural zeros in the cells involving transitions with play markers. Expected values were generated for each table as described on pages 28 and 29, and chi-squared tests with one degree of freedom were applied to individual cells after collapsing the matrix to a 2 x 2 table around the relevant cell (Rechten and Fernald, 1979).

Reference

Rechten, C. and Fernald, R.D. (1979) A sampled randomization test for examining single cells of behavioural transition matrices. Behaviour 69, 217-227.